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FRÅN  
LUNDS GEOLOGISK-MINERALOGISKA INSTITUTION

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# NON-CRINOID PELMATOZOA FROM THE PALEOZOIC OF SWEDEN

A TAXONOMIC STUDY

BY  
GERHARD REGNÉLL

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LUND 1945  
CARL BLOMS BOKTRYCKERI



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A TAXONOMIC STUDY

ACADEMICAL DISSERTATION

BY

GERHARD REGNÉLL

FIL. LIC., LD.

BY DUE PERMISSION OF THE PHILOSOPHICAL FACULTY OF THE  
UNIVERSITY OF LUND TO BE PUBLICLY DISCUSSED IN THE GEO-  
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DEGREE OF DOCTOR OF PHILOSOPHY

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LUND 1945

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Clichés: A.-B. ALMQUIST & CÖSTER,  
Hälsingborg.



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## Preface.

The scope of the present paper is to offer a taxonomic survey of Cystoidea and other non-crinoid Pelmatozoa contained in the Paleozoic deposits of Sweden. The author's intention has been to bring forth the knowledge of these interesting organisms to a point of view answering modern claims. If this aim has been reached to some degree, it is largely thanks to the support of several persons.

The author is greatly indebted, first to Dr J. E. HEDE, Lund, who introduced him into paleontological and stratigraphic research and followed his investigations with never failing interest and spent a lot of time and labour to facilitate the performance of the work; as director of the Paleontological department of the Geological-Mineralogical Institute of Lund, Dr HEDE placed at the author's disposal all the fossil material wanted of this institute.

Thanks are further due to the following persons: —

To Professor A. HADDING, chief of the Geological-Mineralogical Institute at Lund, who in equal way supported the investigation, i.e. by permitting the author to have the main part of the photo-technical work performed and the slides prepared at the institute.

The author tenders his sincere gratitude to these teachers of his for stimulating teaching, inspiring discussions, and great personal kindness through the years.

To Professor E. STENSIÖ, Stockholm, who induced the author to begin the study of cystoids and entrusted to him the elaboration of the large collections kept in the Paleozoological dept. of the State Museum of Natural History, containing the HISINGER and the ANGELIN collections also.

To Professor G. SÄVE-SÖDERBERGH, Uppsala, who placed at the author's disposal a fine collection from the Paleontological Institute, containing also a few interesting specimens of the WAHLENBERG collection.

To Dr P. THORSLUND, Stockholm, keeper of the Museum of the Geological Survey, who committed to him the examination of the cystoids of this museum. The writer is also indebted to Dr THORSLUND for valuable information in different respects.

To Professor T. GISLÉN, Lund, who took great interest in this investigation. The author is particularly indebted to Prof. GISLÉN for useful criticism of the chapters on classification and morphology. The author has profited very much from kind information on the matter given by Prof. GISLÉN and from valuable suggestions made by him.

To Dr A. HOLMBERG, Stockholm, who cared for SVEN LOVÉN's manuscript in the Royal Swedish Academy of Science being placed at his disposal.

To Dr N. ZENZÉN, Stockholm, who gave valuable information on the representation of Cystoidea in several older collections.

The author is also much indebted to Mrs INGRID NILSSON, who undertook the production of most photographs for the present paper. Part of the photographic work was carried out by Mr G. HULTZÉN. Further to Mr G. OLAI, Miss BIRGITTA REGNÉLL, and Dr C. G. REGNÉLL for valuable help on the manuscript and the proofs.

With the exception of a few species, non-crinoid pelmatozoans are met with but occasionally in the Paleozoic strata of Sweden. Several localities, e.g. Norra Freberga (the exposures in the old quarries have not been available for a long time; cf. TÖRNQUIST 1875, p. 66) and Kungs Norrby in Östergötland, from where a good deal of the old collections has been brought together, are no more productive. Owing to this, the author's field-observations and own collecting have not been as extensive as might have been desired. So the investigation has been necessarily based for the greatest part on the fossil material kept in the museums of this country. Like most older collections, however, these have unfortunately one drawback, namely inadequate labelling. The finding places are often too vaguely indicated, and information on the stratigraphic horizons — if present at all — is usually insufficient. This, of course, is very inconvenient in the first hand for the determination of the stratigraphic range of the species.

Isolated stems of pelmatozoans and detached stem-fragments have not been considered in the present study, unless referable with sufficient probability to an appointed species.

For indicating the several museums in which the fossil material placed at the author's disposal is stored the following abbreviations are used: —

LM=Museum of the Geological-Mineralogical Institute of Lund.

RM=State Museum of Natural History, Paleozoöl. dept., Stockholm.

SGU=Museum of the Geological Survey of Sweden, Stockholm.

UM=Museum of the Paleontological Institute of Uppsala.

The author feels it a serious deficiency not to have had occasion to study the very important pelmatozoan collections of several institutes abroad. But war-time conditions rendered every aspiration in that direction impossible. For the same reason the author has not succeeded in procuring certain interesting papers dealing with the matter.

It is the writer's hope that he will get an opportunity to continue his researches into these organisms and to take up several questions — others than the purely taxonomic ones — connected with Swedish Paleozoic pelmatozoans.

# Historical Survey of the Knowledge of non-Crinoid Pelmatozoa.

## Contributions by Swedish Authors.

In 1772 there appeared in the journal of the Royal Swedish Academy of Science a paper by the miner JOHAN ABRAHAM GYLLENHAAL,<sup>1</sup> being a 'Description of the so-called crystal-apples and lime-balls as petrified animals of the genus *Echinus*, or its nearest relatives' (translated from the Swedish by the present author). This article, accompanied by two plates (reproduced here as text-figs. 1—2), is a remarkably fine investigation — in several respects ahead of the times — in which the organic nature of the cystoids was first recognized. Two species were described: *Echinus pomum* and *E. auriantium*, now referred to the genera *Sphaeronites* and *Echinosphaerites* respectively. Speculations regarding mode of life and an account of the peculiar way of fossilization are also contained as well as statements as to the regional distribution of these organisms in the Paleozoic strata of Sweden. On the other hand GYLLENHAAL had not arrived at divesting his mind of the current idea of fossils as still living in recent seas. Nor is it any wonder that the cystoids were looked upon as sea-urchins.<sup>2</sup> About GYLLENHAAL's interpretation of the thecal openings, cf. p. 58 below.

The globular bodies of *Sphaeronites* and *Echinosphaerites* occurring so abundantly in certain rocks had not failed to be noted by earlier Swedish observers, but they were invariably thought to be of inorganic origin. Thus they were mentioned under various names by LINNAEUS (1745, pp. 136, 156: — "Crystall-äplen"; 1753, p. 78: — "Aetites. Örnsten",<sup>3</sup> p. 81: — "Pomum

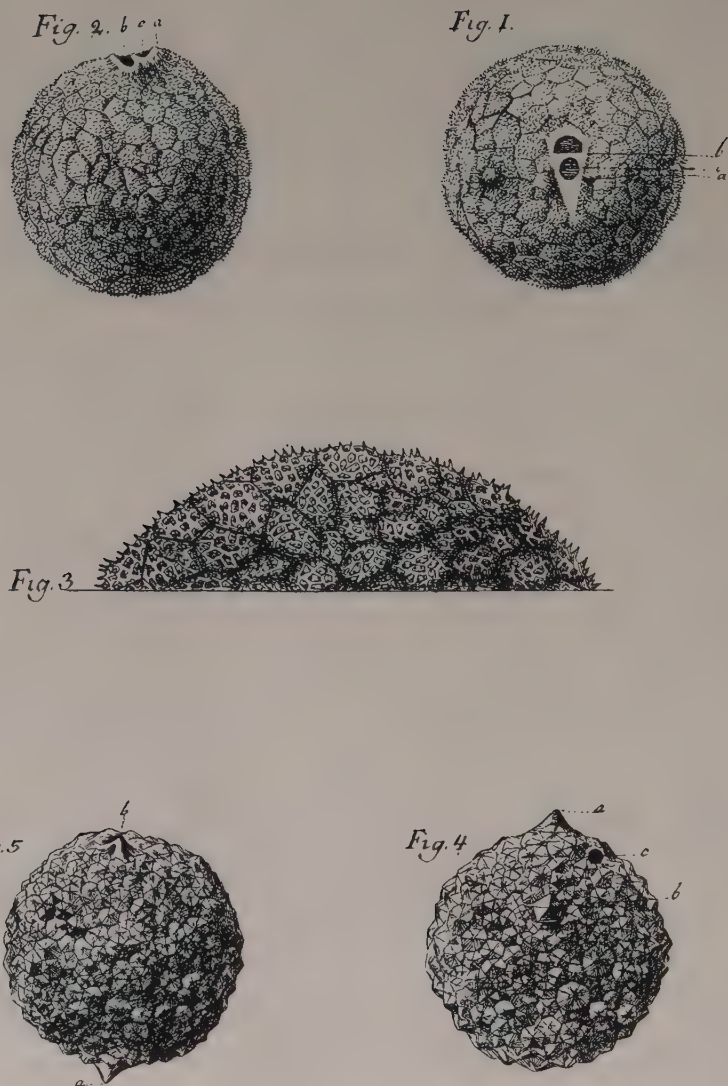
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<sup>1</sup> The name ought to be written in the way here used, with double a, though in the heading of the quoted paper it is spelt GYLLENHAHL.

<sup>2</sup> A true fossil echinoid was, however, also described by GYLLENHAAL in a manuscript, the main part of which was never printed. An abstract, containing the diagnosis of "*Echinites areolatus*" [= *Salenia areolata* (WAHLENBERG)] was published by WAHLENBERG (1821, pp. 45—48), many years after GYLLENHAAL's death.

<sup>3</sup> "Aetites" of ancient and mediaeval writers apply to concretions known as "Klappersteine", i.e. concretions deposited around some nucleus which owing to shrinking or some





Text-fig. 1. Reproduction of Pl. 8 accompanying GYLLENHAAL's paper of 1772. The explanations of figs. were given thus: 1—2. *Echinus pomum* in different positions; a=peristomal-periproctal area, b=mouth, c=anus. 3. Magnified portion of the same animal. 4. *Echinus Aurantium* var.  $\alpha$ ; a=rostrum inferius [peristomal projection], b=os [anus], c=anus [gonopore]. 5. The same variety; a=rostrum inferius [peristomal projection], b=rostrum superius [aboral pole]. Slightly reduced.

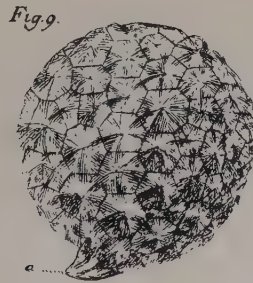
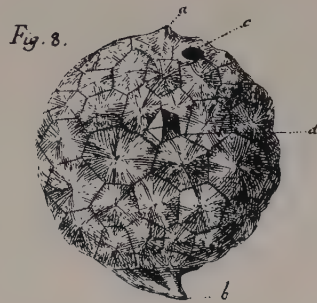
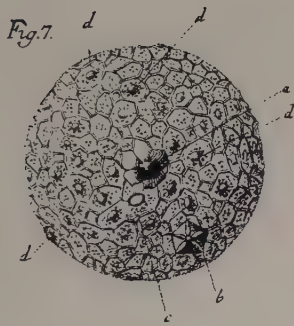
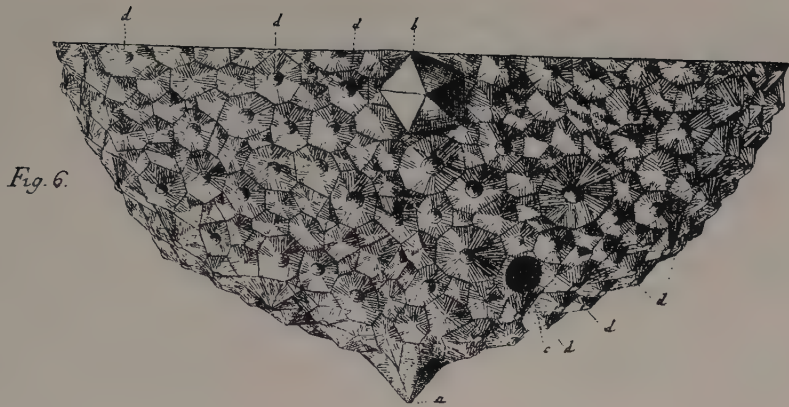


Fig. 10.



Text-fig. 2. Reproduction of GYLLENHAAL's Pl. 9, of which the following explanations were given: 6. Magnified portion of *Echinus Aurantium* var. α; a=rostrum inferius [peristomal projection], b=os [anus], c=anus [gonopore], d=glandula valvularum [umbo of plates]. 7. The same variety, mould; lettering as in the preceding. 8. *Echinus Aurantium* var. β; a=rostrum inferius [peristomal projection], b=rostrum superius [aboral pole], c=anus [gonopore], d=os [anus]. 9. The same variety; a=rostrum superius [aboral pole; no explanation of this fig., and of figs. 8 c—d, was given by GYLLENHAAL]; 10. "Major plates of a foreign echinit". Slightly reduced.

crystal. crystalläple”), LINNÉ (1768, pp. 179, 180: — “Aetites marmoreus, crystal-äple”), KALM (1746, p. 28: — “Crystall-äplen”), WALLERIUS (1747, p. 62: — “Spat-klot”), and by CRONSTEDT in his anonymously edited textbook of mineralogy (1758, p. 11: — “Spat-klot”).<sup>4</sup> A specimen of *Echinosphaerites aurantium* was figured already by TILAS (1740, Pl. 2, fig. 18); it was not referred to in the text,<sup>5</sup> however.

During his travels in Sweden in the beginning of the 19th century, W. HISINGER had many occasions to study the common forms of cystoids and communicated in his writings several observations on these fossils, especially regarding their distribution. In the Lower Chasmops limestone at Böda in Öland he detected a form later known as *Heliocrinites granatum* (WAHLENBERG). It was figured and described 1802 (pp. 189—190, Pl. 7, fig. b) but not specified by any name. To judge from his description, it seems very likely that HISINGER included in his species also *Caryocystites angelini* (HAECKEL), which is very common at this locality. The last-mentioned species was figured by HISINGER 1831 (Pl. 7, figs. a, a; the figures inverted), again without giving any name, and, finally, in his ‘Lethaea Svecica’ (1837 b, Pl. 25, fig. 8 d) under the name of *Sphaeronites citrus*. Yet it was remarked (op. cit., p. 92) that this form is not of the regular type of the species mentioned. For *Heliocrinites granatum* he used as a synonym of “*Sphaeronites granatum*” the term “*Sphaeronites testudinarius*” (1837 a, p. 115; 1837 b, p. 92), which, owing to a misprint on Pl. 25 in ‘Lethaea Svecica’ (1837 b), was adopted by BUCH (1846 a, p. 107) for what is now called *Caryocystites angelini* (HAECKEL), hereby giving rise to a good deal of confusion in the writings of subsequent authors.<sup>6</sup>

other process comes to lie loose within the external shell, so that it rattles when the concretion is shaken. The stone derives its name “eagle stone” from the fact that eagles were believed to place it in their nests when about to lay their eggs (ADAMS, F. D., 1938. The birth and development of the geological sciences. — Baltimore [WILLIAMS & WILKINS], p. 100).

<sup>4</sup> The editor of the second edition remarked (1781, p. 18): — “Dessa äro petrificater af Sjöäpplen”. Also WALLERIUS remarked in the second part of his ‘Systema Mineralogicum’ (1775, p. 509) that “globuli spathacei et calcarei” in certain cases should be classified as *Echiniti globulares*, whereas in the first part of this work (1772) their mineral character was not doubted.

<sup>5</sup> Dr N. ZENZÉN, with his expert knowledge of the history of geological sciences in Sweden, readily informed the author (in letter) that cystoid specimens (evidently foremost *Echinosphaerites aurantium*) are to be found in several of the mineral-collections from the 18th century. The specimen figured by TILAS (1740) is not preserved. — GYLLENHAAL’s collections were donated to Vetenskaps-Societeten of Uppsala, from where at least part of the paleontological material was handed over to the Paleontological Institute of Uppsala. Prof. SÄVE-SÖDERBERGH very kindly had the cystoids searched for, but, if still preserved, they have not been traced as yet. Thus we likely have to consider GYLLENHAAL’s original specimens as lost.

<sup>6</sup> There is a fact to be observed at the use of certain older publications (and, of



It deserves to be noted that HISINGER in one instance (1828, p. 195) made a statement about the zoological position of Cystoidea, which means a progress from the earlier conception of the matter. He declared (l.c.) that they should be placed between the "Encrinites" (=Crinoidea) and "Echinities" (=Echinoidea), "såsom begåfvade med stjelkar och ett slags knoppar, svarande mot Encriniternas kronor" ["being provided with stems and a sort of buds, corresponding to the crowns of Encrinites"]. — Here also the generic name *Sphaeronites* was introduced. HISINGER's fossil-collection is now in the State Museum of Natural History, Stockholm. Most of his original specimens cannot, however, be recognized.

The generic name *Echinosphaerites* was introduced in literature by WAHLENBERG 1818 (p. 44). In *Echinosphaerites* he included the two species described by GYLLENHAAL. In his well-known treatise 'Petrificata telluris Svecanae' he also referred to *Echinosphaerites* the anonymous species of HISINGER 1802, for which he adopted the name *E. granatum* (WAHLENBERG 1821, p. 53). This species is now referred to *Heliocrinites* EICHWALD and "*Echinosphaerites*" *pomum* to *Sphaeronites* HISINGER. In describing the series of strata of the Paleozoic of Västergötland, WAHLENBERG (1818, p. 44) observed the different stratigraphic range of *Sphaeronites pomum* (GYLLENHAAL) and *Echinosphaerites aurantium* (GYLLENHAAL).<sup>7</sup> WAHLENBERG was aware of the fact that the cystoids in question differ from the true »Echini», the plates of their test not being radially arranged and not bearing any spines. It was not suggested, however, that they might be related to the Crinoidea. — In the WAHLENBERG collection, kept in the Paleontological Institute of Uppsala, there are not more than eight specimens of cystoids, all belonging to the three species mentioned.

The eminent echinodermologist SVEN LOVÉN felt a deep interest in cystoids, though unfortunately not very much of his studies got ready for

course, certain more recent publications reproducing old figures), viz. that the figures are images, on account of which right and left are shifted. This does of course matter only in figures of forms with unpaired organs holding a strictly orientated position. Thus e.g. the anal aperture of *Echinosphaerites aurantium* is seen to lie to the right of the gonopore, whereas in reality it is to the left of the observer. This inadvertency is met with e.g. in GYLLENHAAL 1772, Pl. 9, figs. 6—7 (cf. our text-fig. 2), in HISINGER 1837 b, Pl. 25, fig. 8 a, in PANDER 1830, Pl. 2, fig. 21, Pl. 29, fig. 2 a, ZITTEL 1924, figs. 337 a—b, and SPRINGER 1913, figs. 238 a—b. The lithographer obviously reproduced the original drawing on the stone without making corrections for the figures being inversed at the printing of the plate. This, moreover, can be stated directly in the case of ZITTEL's fig. 337 c (=SPRINGER's fig. 238 c) which is an inverted copy from VOLBORTH 1846, Pl. 9, fig. 6. In certain instances the reversion may be due to the fact that a camera lucida was used at the drawing, resulting in reversed images, as observed by BASSLER (1935, p. 1).

<sup>7</sup> Curiously enough the Silurian graptolite shales were said to rest upon the Orthoceratite limestone and to be covered by the *Echinosphaerites*-bearing *Chasmops*-layers, upon which the dolerite was said to follow.

publication. His first notes on this matter appeared in a small treatise of 1867, in which the spatangoid echinoid "*Leskia*" [*Palaeostoma*] *mirabilis* GRAY from the seas around the Malay Archipelago was redescribed. Already GRAY had pointed out the supposed affinity with cystoids as to the form of mouth and anus. His suggestion was confirmed by LOVÉN after a careful examination of the ambulacral area and adjacent portions in *Sphaeronites pomum* and *Echinosphaerites aurantium*. LOVÉN was the first to recognize the gonopore as an "external genital organ" (1868, p. 181); he found also a certain indication of the possible existence of a madreporite, an organ which VOLBORTH (1846, p. 189) many years before had observed in *Glyptosphaerites leuchtenbergi* (VOLBORTH), though with some hesitation as to its nature. Less successful was LOVÉN in his interpretation of the anal pyramid which he thought — in accordance with BILLINGS (1858, pp. 15, 32) — to be the mouth that had also undertaken the anal functions. Objection against this theory was raised by CHR. LÜTKEN, who communicated an abstract of LOVÉN's paper in the Geological Magazine (LOVÉN 1868). There he emphasized (op. cit., p. 182) that the mouth of all living echinoderms lies in the centre of the ambulacral system, where most students had assumed it to lie even in the Cystoidea. The mistake was admitted by LOVÉN 1883 (p. 28, foot-note 1).

LOVÉN pretended to have found reminiscences of the Cystoidea even in another recent echinoderm, dredged at Cape York, Torres Strait, which he described under the name of *Hyponome sarsi* (1869). In the English version of his paper, expanded in a few points, this form was plainly characterized as a "recent Cystidean". Certain organization features were said to recall those of different cystoid genera. This view was corroborated by VOLBORTH (1870, p. 8). WYVILLE THOMSON, as communicated by CARPENTER 1879 (p. 388), unmasked *Hyponome* as the ejected viscera and disc of a comatulid. The species in question should be referred to *Zygometra* A. H. CLARK and, according to A. H. CLARK (1918, p. 60), possibly to *Z. microdiscus* (BELL).

There are also some remarks on the morphology of Cystoidea in LOVÉN's memoir of *Pourtalesia* (1883).

Through a statement in G. LINDSTRÖM's obituary of SVEN LOVÉN, the present writer became aware of the possible existence of an unprinted work by LOVÉN dealing with Cystoidea. LINDSTRÖM (1895, p. 638) stated that in LOVÉN's scientific remains there was an unfinished manuscript on Cystoidea, the preparation of which had been in progress during some 25 years. The text was said to have been partly ready for the press, as well as fifteen lithographed plates. At the request of the present author, the Librarian of the Royal Swedish Academy of Science, Dr A. HOLMBERG, kindly gave the information that the Academy possesses 22 sheets (sign. Ms. LOVÉN, Sv.), being notes on Cystoidea by LOVÉN, and a box containing original drawings

for a projected paper on Cystoidea (sign. Ms. Pl. v. 54). Thanks to the courtesy of the Board of the Academy, the author got an opportunity of examining these notes and drawings. Thereby it turned out, however, that the manuscript sheets have but little interest, for they are solely excerpts, 14 of them regarding Edrioasteroidea and 8 regarding Blastoidea. Hydrophoridea are represented on 9 plates. This material could evidently not be that alluded to by LINDSTRÖM. Dr HOLMBERG, therefore, was so kind as to undertake a thorough search for the wanted manuscripts, which met with success in so far as a volume of 16 lithographed plates was located to the Paleozoological department of the State Museum of Natural History. The volume has the annotation (here translated from the Swedish): 'Unpublished plates to an unaccomplished work by Prof. S. LOVÉN on Cystoidea'. It is now in the library of the Academy of Science (sign. Ms. Pl. v. 188). Unfortunately enough, the accompanying text remained undiscovered. There is no doubt, however, that the plates are those searched for. All figures of cystoids present in the original drawings mentioned above are to be found on the lithographed plates. They are exceedingly well and — in most cases — accurately executed. A survey of their contents will follow, maintaining the order in which the plates are arranged in the volume. In cases where it has been possible to identify the original specimens, kept in the State Museum of Natural History, their numbers are given: —

- Pl. 1 (5 figs.). "*Hyponome*" (*Zygometra*) *sarsi* LOVÉN (cf. above); Torres Strait.  
 „ 2 (2 figs.). *Callocystites jewetti* HALL.  
 „ 3—4 (12 figs.). *Protocrinites fragum* EICHWALD.  
 „ 5 (13 figs.). *Glyptosphaerites leuchtenbergi* (VOLBORTH); after specimens in the then Imp. Academy of Sciences of St. Petersburg.  
 „ 6 (2 figs.). *Lovénicystis angelini* (JAEKEL) (= "*Lepadocrinus gebhardi*" ANGELIN, non HALL), Gotland.  
 „ 7—8 (23 figs.). *Protocrinites fragum* EICHWALD.  
 „ 9. 1. *Sphaeronites pomum* (GYLLENHAAL), Boda(?), Öland [RM Ec 4186]. 2. Id. species, id. loc. [RM Ec 4187]. 3. Id. species, id. loc. [RM Ec 4188]. 4—5. *Sphaeronites globulus* (ANGELIN), id. loc. [RM Ec 4193]. 6. *Haplosphaeronis* sp., Fjäckå, Dalarna [RM Ec 115]. 7. *Sphaeronites pomum*, Boda(?), Öland [RM Ec 4189]. 8. Id. species, id. loc. [RM Ec 4190]. 9. Id. species. 10. *Eucystis* sp., Arvet, Boda, Dalarna [RM Ec 2371].  
 „ 10. (The numbering of the figures was performed by the present writer). 1. *Haplosphaeronis oblonga* (ANGELIN), Fjäckå, Dalarna [RM Ec 116]. 2. Id. species. 3 a—c. *Eucystis angelini* LOVÉN MS., Boda, Dalarna [RM Ec 2375]. 4 a—b. *Eucystis raripunctata* ANGELIN, Arvet, Boda, Dalarna [RM Ec 2376].  
 „ 11 (13 figs.). *Callocystites jewetti* HALL.  
 „ 12 (6 figs.). *Glyptocystites multiporus* BILLINGS.  
 „ 13 (18 figs.). *Lovénicystis angelini* (JAEKEL) (= "*Lepadocrinus gebhardi*" ANGELIN, non HALL), Gotland. It has not been possible to trace the original specimens in all instances. Figs. a—d (lettering by the present author; cf. text-fig. 16) show a restored specimen, the stem of which is drawn from RM Ec 5039; fig. p (maybe also part



- of a—d) = RM Ec 5040; figs. h, l = RM Ec 5041; figs. g, m (likely also part of d) = RM Ec 5035 (which is also original of ANGELIN 1878 a, Pl. 19, fig. 18); fig. n = RM Ec 5034? (= ANGELIN, Pl. 11, figs. 30—34).
- Pl. 14 (10 figs). *Mesocystis pusyrewski* (HOFFMANN); after a specimen in the then Imp. Academy of Sciences of St. Petersburg.
- „ 15 (5 figs.). *Edrioaster buchianus* (FORBES); after specimens in the Museum of Practical Geology, London.
- „ 16 (6 figs.). *Hemicystites bohemicus* (F. ROEMER); after specimens in the Museum für Naturkunde, Berlin (figs. 1—2, 4—5), and Prague (fig. 3). On this plate is written “Lithogr. 1891”.

In order to give an idea of the extent of LOVÉN's projected paper on Cystoidea, evidently partly prepared but unfortunately lost, the writer has thought it desirable to make the above list as complete as possible, with the aid of the fragmentary annotations in the handwriting of LOVÉN on the plates, the figures themselves, and the original specimens as far as identified.

The material to hand thus consists of the following Rhombifera and Diploporita: — Five genera occurring in Sweden, viz. *Lovénicystis*, *Glyptosphaerites* (Russian specimens only), *Sphaeronites*, *Haplosphaeronis*, and *Eucystis*; two genera occurring in USSR and Estonia: — *Protocrinites* and *Mesocystis*; one genus occurring in Canada: — *Glyptocystites*; one genus occurring in North America: — *Callocystites*. Besides that, there are two genera of Edrioasteroidea: — *Edrioaster* (Great Britain) and *Hemicystites* (Bohemia), and, finally, one genus of Crinoidea: — *Zygometra*, “the recent cystoidean”.

The morphological features of the specimens studied are extremely carefully observed and reproduced, though in some instances the figures must be said to be too beautiful and too full of details, showing more than is to be seen in the actual specimens. The present author hopes he will be able — with due permission — to render justice below in some points to this fine material.

It was not granted to SVEN LOVÉN to complete this broadly planned investigation, but his name is nevertheless connected with the only hitherto existing monographic revision of Swedish Cystoidea included in ANGELIN's ‘Iconographica crinoideorum’ (1878 a), the section on “Crinoidea propria” being edited by G. LINDSTRÖM, that on “Cystidea” by LOVÉN.

ANGELIN's work meant a considerable progress in the knowledge of Cystoidea in general and their Swedish representatives in particular. Its style is very concentrated, however, the chapter on Cystoidea comprising less than five pages in folio. Nine genera with 23 species were described and illustrated on lithographed plates. Three species were figured after material from USSR without being mentioned in the text. These are: — *Glyptosphaerites leuchtenbergi* (VOLBORTH) (Pl. 11, figs. 1—4), *Crypto-*

*crinites laevis* (PANDER) (Pl. 12, figs. 1—5), and "*Echinoëncrinus Senckenbergi* H. v. MEYER" (Pl. 12, figs. 6—12; Pl. 13, figs. 1—3; cf. below).

It is quite natural that ANGELIN's delimitation of genera and species in many cases does not answer the claims of modern taxonomy. The figures are in general rather rough (»ANGELIN's notoriously inaccurate figures», BATHER 1900, p. 72), which might have given rise to some mistakes by subsequent authors. Yet, as stated BATHER (1893, p. 4), "historically regarded this book of ANGELIN's is a magnificent production". Part of the Crinoidea, viz. the Inadunata, was revised by BATHER 1893. Great attention was paid to the Cystoidea by JAEKEL 1899.

According to the international rules of nomenclature most generic names used by ANGELIN have to be rejected. All names ending in *-ites* were namely changed with reference to the proposed fact that "Nominum genericorum exitus in *ites*, regno lapideo principio proprius, regno animali alienus" (ANGELIN 1878 a, p. 28). Cf. also p. 31 below.

ANGELIN's collection is preserved in the State Museum of Natural History, Stockholm.

A few interesting finds of Cystoidea were communicated by HOLM. In 1882 (p. 68) he reported a "*Glyptocystis*" (= *Cheirocrinus holmi* n. sp.) from the Lower Ordovician of Öland and in 1890 a *Caryocrinites* from the "Leptaena limestone" of Dalarna. The first-mentioned species is remarkable as the oldest cystoid known from Sweden, and the second as a representative of a genus known till then as exclusively American. Later the genus was recorded from Norway (KIAER 1897) and Burma (BATHER 1906), too.

In 1892 C. W. S. AURIVILLIUS published an investigation of Silurian "cirripeds" from Gotland. Among these were seven species of "*Scalpellum*" which were removed from the "cirripeds" by BATHER (1915 a) and placed in the genus *Pyrgocystis* (Edrioasteroidea) established by himself. The number of species was reduced to three. Several modifications of the Swedish species as conceived by BATHER have, however, proved necessary.

The papers of WIMAN 1907 b and SJÖBERG 1915 announced some unique specimens, viz. a stem-fragment undoubtedly belonging to *Dendrocystites*, respectively a species of — as was supposed — uncertain systematic position, described as *Paracystis ostrogothicus*. The first-mentioned, from boulders of the West Baltic "Leptaena limestone", is one of the two remains of Carpoidea traced in Swedish Paleozoic strata,<sup>8</sup> and the second, from the Chasmops limestone of Östergötland, one of the two known representatives of Blastoidea coronata in Sweden.

<sup>8</sup> Another species, "*Ateleocystis Huxleyi* BILLINGS", was mentioned by LINDSTRÖM 1888 b (p. 20) from the Silurian of Gotland. From reasons unfolded below it may be inferred that LINDSTRÖM's species, which was recorded in a faunal list without description or figure, cannot possibly have been *Ateleocystites huxleyi* BILLINGS.

The above review may have given an account of the most important contributions by Swedish authors to the taxonomy of Swedish non-crinoid *Pelmatozoa*. Parenthetically may be mentioned that LINNARSSON (1871 a) called attention to the presence of a certain organism in the Lower Cambrian "Eophyton" [Mickwitzia] sandstone of Västergötland, which was looked upon as an edrioasteroid and described as "*Agelacrinus? Lindströmi*". The generic determination was confirmed by LOVÉN (LINNARSSON 1871 a, p. 12). In 1881 (p. 5)<sup>9</sup> NATHORST showed its nature of a cast of a medusa, now referred to *Medusina costata* (TORELL). LOVÉN later accepted this view (NATHORST 1881, p. 5).

A lot of notes concerning the stratigraphic range and regional distribution of *Cystoidea* is contained in the writings of many authors which of course cannot be listed here.

At the end of this chapter the author wishes to point at the very fertilizing ideas set forth by GISLÉN (1930) regarding the suggested importance of *Carpoidea* for the phylogenetic evolution of *Chordonia*. In other publications also (GISLÉN 1934 &c.) the same scientist considered non-crinoid *Pelmatozoa* in approaching problems of fundamental significance.

### Development of the Knowledge of non-Crinoid *Pelmatozoa* outside Sweden.

It has been thought useful to review on the preceding pages in one connexion the principal contributions by Swedish scientists to the knowledge of non-Crinoid *Pelmatozoa*. In that way we might also have obtained an idea of the present knowledge of the Swedish representatives of that group. For, as a matter of course, Swedish writers have usually studied material from their own country, whereas their colleagues abroad have made only few and occasional remarks on the same subject.

One of the first continental writers who described cystoids, KLÖDEN 1834, remarked that the study of these organisms had begun in Sweden. He wrote about "Echinosphäriten" (op. cit., p. 240): — "Dies ganze Geschlecht seltsamer und offenbar sehr alter Naturkörper, von welchem bisher drei Arten bekannt geworden sind, ist, so weit unsere Kenntnisse dermalen reichen, nur auf Schweden und Esthland beschränkt, und ausserdem ein Vorkommen nur noch in Deutschland durch v. MEYER bekannt, weshalb auch nur die nordischen Naturforscher von denselben sprechen, unsere westlichen und südlichen Nachbarn aber von denselben fast gänzlich schweigen." That KLÖDEN did not mention the paper of SAY 1825 on *Caryocrinites*

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<sup>9</sup> NATHORST, A. G., 1881. Om aftryck af medusor i Sveriges kambriska lager. — K. V. A. Handl. 19: 1. Stockholm. Pp. 1—34. Pls. 1—6.



might be due to the fact that this genus was considered a crinoid. He overlooked the paper of SCHLOTHEIM 1826. KLÖDEN himself was not absolutely acquainted with the habit of cystoids, however, as appears from his supposition (pp. 285—286) that a specimen, later recognized as the alga *Coelosphaeridium cyclocrinophilum* F. ROEMER,<sup>10</sup> might represent "*Echino-sphaerites Pomum* WAHLENB."<sup>11</sup>

There is no reason to give a full account of the literature, all the more as an almost complete list in chronological order was compiled by JAEKEL 1899 (pp. 437—441). Only certain important papers will be shortly reviewed.

H. v. MEYER's announcement of *Echinoencrinites senckenbergii* (1826) was mentioned already by KLÖDEN. The very rich cystoid faunas of the East Baltic provinces were further made known to science through the publications of SCHLOTHEIM 1826, EICHWALD 1829—1860, PANDER 1830, VOLBORTH 1842—1870, LEUCHTENBERG 1843, VERNEUIL 1845, and F. SCHMIDT 1874—1880.<sup>12</sup>

Cystoid material from the East Baltic provinces was also made use of by L. v. BUCH, whose paper of 1846 (1846 a) is a mile-post on the way to a correct understanding of these fossils, although in certain points he was wrong in his interpretation of their organization (cf. below, p. 17). And it must be admitted that the authority of BUCH delayed the rectification of some misconceptions in his investigation. Anyhow, several species were closely described and, what is more important, those puzzling bodies were joined under the name of Cystoidea and characterized diagnostically (1846 a, p. 101). The differences between Cystoidea and Crinoidea were discussed. Some years later, the Cystoidea were put in relation to Echinodermata on the whole by the great founder of modern echinodermology, JOHANNES

<sup>10</sup> Cf. STOLLEY, E., 1896. Untersuchungen über *Coelosphaeridium*, *Cyclocrinus*, *Mastopora* und verwandte Genera des Silur. — Arch. Anthropol. Geol. Schlesw.-Holst. 1: 2, pp. 178, 179.

<sup>11</sup> Another genus of algae, *Cyclocrinites*, was referred to the Hydrophoridae by EICHWALD (1840, p. 204; 1860, p. 638). Later authors, e.g. NICHOLSON 1879 (p. 297), called in question its belonging there but placed it, together with some other algae, in the vicinity of the "Cystoidea".

<sup>12</sup> The so-called platysolenites from the Lower Cambrian blue clay of the East Baltic area were looked upon by SCHMIDT as stems or brachioles of cystoids, which may be mentioned, since the same interpretation was repeated tentatively still 1931 in the last edition (pt. 2, p. 306) of RAMSAY's text-book of geology — well-known to students of Swedish tongue. BASSLER (1911, p. 10) and SCUPIN (1928, p. 171) also took them as pelmatozoans. This theory was disproved definitely by M. JANISCHEWSKI (Sur les restes des Tubicola de l'argile cambrien. — Ann. Soc. Paléontol. Russie. 4. 1922—24. Leningrad 1926), who referred the platysolenites to Annelida tubicola (cf. also R. HECKER, 1928. Ueber Akademiker Fr. Schmidt's Ansicht inbetreff der Natur der Platysoleniten, &c. — Ann. Soc. Paléontol. Russie. 7. 1927. Leningrad 1928).

MÜLLER. Many fine observations on Cystoidea are enclosed in his admirable treatise 'Über den Bau der Echinodermen' (1854).

BUCH's (and later MÜLLER's) investigation of the morphology of cystoids caused scientists in several countries to take an inventory of the cystoid fauna. Thus monographs were produced, on the British Ordovician and Silurian forms by E. FORBES (1848), on the Ordovician forms of Canada by BILLINGS (1858 a), and on the Paleozoic forms of Bohemia by BARRANDE (1887).<sup>13</sup> North American species were examined by HALL (1852 &c.). LORETZ (1884) gave information of Cystoidea from Thüringen, and KOENEN (1886) described new species from France.

The years around the turn of the century brought some fundamental works: — JAEKEL's monumental treatise of 1899, which was preceded by some smaller contributions by the same author, and BATHER's well-known text-book of 1900. In the field of echinodermology, JAEKEL and BATHER are the great authorities on fossil material, and their research, continued through a long series of years, meant a mighty advance of the knowledge of Cystoidea. In many points their views came apart but in material respects they arrived on different ways at coincident opinions. JAEKEL's treatise, a magnificent volume of about 450 pages in quarto, presented a classification of Cystoidea (and Thecoidea, or Edrioasteroidea, which were thought equal to Cystoidea in taxonomic rank), founded on a penetrating morphological analysis. For the preparation of this work JAEKEL had at his disposal a good deal of the cystoid material collected up to then, also that of the State Museum of Stockholm (9 genera were mentioned from Sweden, p. 153). It was followed by an investigation in which the Carpoidea were characterized (JAEKEL 1900). BATHER's text-book gained a special importance through his being an active student of echinoderms of different classes, fossil as well as recent. This hand-book is also still the last one treating extinct echinoderms side by side with living ones.<sup>14</sup> An epitome of the classification of the Pelmatozoa had been presented some time before the appearance of the text-book (BATHER 1899).

Some years before the standard works just mentioned, there appeared a paper on Cystoidea by E. HAECKEL (1896). It was received with severe criticism and it is undoubtedly impaired by serious errors, owing to HAECKEL's insufficient familiarity with the actual fossil material. So JAEKEL's final judgment (1897, p. 395) seems to be appropriate: — "An geistreichen Anregungen ist dem kritischen Leser in dem vorliegenden Werke unstreitig

<sup>13</sup> A revised nomenclature (in accordance with JAEKEL 1899) of the species described by BARRANDE was presented by PERNER 1900.

<sup>14</sup> A predecessor of BATHER's treatise is that of DUJARDIN & HUPÉ 1862. In the section Echinodermata of The Cambridge Natural History, written by A. W. MACBRIDE (1906) a certain attention is paid to fossil forms also.

viel geboten, aber das reale Ergebniss der veröffentlichten Forschungen ist ein sehr bedenklich gestütztes Gebäude der Phantasie."

For the many contributions to the knowledge of taxonomy, ecology, &c. of Cystoidea offered by JAEKEL and, in particular, by BATHER, it may be referred to the list of publications at the end of the present paper. Only a few should be pointed at here: — BATHER's treatises of 1906 and 1913 on Ordovician cystoids from Burma and Girvan respectively, in which many species were described and many taxonomic questions brought up for discussion; BATHER's 'Studies in Edrioasteroidea' and his 'Notes on Yunnan Cystoidea' published in the Geological Magazine; and JAEKEL's 'Phylogenie und System der Pelmatozoen' (1918). In the last-mentioned paper the systematic arrangement of Cystoidea was not very much altered from the work of 1899. It is important, however, that the Blastoidea were now registered as a subclass of Cystoidea, and that the earlier, more provisional notes on the Carpoidea, which were looked upon as a separate class, were now expanded and systematized. The treatise was intended to form the completion of 'Stammesgeschichte der Pelmatozoen', of which part 1 appeared in 1899. But unfortunately JAEKEL did not find time enough for so careful a preparation as required the topic. Especially he has been blamed, rightly, for introducing in a synoptical work like this a great number of new genera and species inadequately diagnosed. Thus the new species were usually characterized by text-figures only and the new genera by too brief diagnoses (cf. W. E. SCHMIDT 1923). Very likely JAEKEL saw no other possibility to get the many new forms and his final views of the system of pelmatozoans published at all. A few smaller contributions followed, however, two of them communicating Swedish specimens (JAEKEL 1927 a, 1927 b).

During the last decades, the good traditions from EICHWALD, VOLBORTH, F. SCHMIDT, and other scientists of Russia and the East Baltic Provinces have been well upheld, especially by JAKOVLEV and HECKER. The first-mentioned approached morphological and phylogenetic problems, whereas the latter dealt with his material from a faunistical and paleobiological point of view. Also ORVIKU's investigation concerning *Echinosphaerites aurantium* (1927 b) may be referred to in this connexion.

DEHM (1933, 1934) and RICHTER (1930) published fine studies of peculiar forms from the Devonian of Germany. THORAL (1935), DREYFUSS (1939), CHAUVEL (1941, &c.), and others elaborated the cystoid and carpoid faunas of France. Among American students of those organisms, SCHUCHERT (papers 1903—1919) and BASSLER stand out. The taxonomist owes a good deal of gratitude to BASSLER for his 'Bibliographic index' (1915), not to mention his 'Classification of the Edrioasteroidea' (1935), and, in the highest degree, for his 'Pelmatozoa Palaeozoica' (1938), forming a part of the 'Fossilium Catalogus' and being an excellent guide through the labyrinth of nomenclature.



## Classification of the Pelmatozoa.

To get a grip of the Swedish non-crinoid pelmatozoans it is necessary to scrutinize the whole subphylum of the Pelmatozoa.

After thorough and unprejudiced consideration the present writer — essentially in agreement with JAEKEL — arrived at the following classification: —

Subphylum Pelmatozoa LEUCKART 1848.

Class Eocrinoidea JAEKEL 1918.<sup>1</sup>

Class Paracrinoidea nov.

Class Cystoidea BUCH 1846, emend. JAEKEL 1918.

Subclass Hydrophoridae ZITTEL 1903 [= Cystoidea auctorum].

Order Rhombifera ZITTEL 1879, emend. BATHER 1899 [= Dichoporida JAEKEL 1899].

Order Diploporita J. MÜLLER 1854, emend. BATHER 1906.

Subclass Blastoidea SAY 1825.

Order Parablastoidea HUDSON 1907 [= Protoblastoidea BATHER 1899, ex parte].

Order Coronata JAEKEL 1918.

Order Eublastoidea BATHER 1899 [= Radiolata JAEKEL 1918; Blastoidea auctorum].

Class Crinoidea J. S. MILLER 1821.

Class Carpoidea JAEKEL 1900, emend. JAEKEL 1918 [= Carpoidea Heterostelea JAEKEL 1900].

Class Edrioasteroidea BILLINGS 1858 (1854),<sup>2</sup> emend. BATHER 1899 [= Thecoidea JAEKEL 1895].

Incertae sedis: Cyclocystoidea MILLER & GURLEY 1895.

At the top of this table is placed the primitive group Eocrinoidea (and in connexion with it the Paracrinoidea) appearing in Lower Cambrian depo-

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<sup>1</sup> In his paper of 1918 (p. 24) JAEKEL gave 1899 as the year of publication for the term Eocrinoidea. This is not correct, however, since the term was not defined and not even mentioned in JAEKEL's memoir of 1899.

<sup>2</sup> Cf. the systematic part below.

sits already. This group lies evidently in the ancestral line of the Cystoidea and Crinoidea, and has been proposed to have given rise to the ancient pelmatozoan branches Carpoidea and Edrioasteroidea too.

It is, in fact, no very easy task to find out which characters may in the first hand be used when trying to get a natural classification of the Pelmatozoa. For in many instances forms are known which are clearly intermediate between groups here referred to as different classes. So the limits between certain classes are not always distinct. Further it must be remembered that characters which are thought to be essential for a certain group, e.g. the presence or the absence of exothecal skeletal appendages, or the presence or the absence of thecal pores, may have been acquired quite independently in different evolution lines. In such cases it may happen that forms which are indeed not very closely related are brought together into one taxonomic unit. Especially may degeneration phenomena give rise to forms that are disposed for being mistaken for primitive organisms. As, however, the actual morphologic appearance is the only basis available for the classification, and the uninterrupted evolution line of a form-series is possible to trace but very seldom, this kind of errors are exceedingly hard to detect and to avoid.

The opinions of the earlier authors as to the classification of the Pelmatozoa need not be dealt with here at some length, since they have been discussed in several papers, foremost by JAEKEL and BATHER, the two authorities whom we owe a good share of our knowledge of these organisms. To the reader acquainted with the literature on the matter, it will be evident that the classification of the Pelmatozoa here adopted agrees as a rule more, as indicated above, with that set forth by JAEKEL than with that advanced by BATHER in points where these two scientists took up different positions.

Before the investigations carried out on Cystoidea (i. e. Hydrophoridea in the sense here used) by L. VON BUCH a hundred years ago, the Crinoidea and the Blastoidea were the only known groups of pelmatozoans. As the knowledge of the subphylum increased by the labour of several scientists, further taxonomic categories were distinguished.

The present author has found himself forced to make certain modifications of the system more or less generally accepted. Thus the arrangement of BASSLER's recent (1938) index of the fossil Pelmatozoa could unfortunately not be accepted in unchanged form.

We will now carry on the discussion to a short review of the divisions here concerned, and it might be appropriate to begin with the cystoids in order to settle, as far as possible, this conception, which seems often to have been taken for a sack into which awkward echinoderms should conveniently be tucked down.

## Class Cystoidea.

The Cystoidea have been subject to different opinions as to their systematic position and the range of the group among the Pelmatozoa.

The first author to describe cystoids, GYLLENHAAL (1772), referred them, as was already mentioned (p. 1), to the Echinoidea. The same view was held by EICHWALD in his 'Zoologia specialis' (1829), where *Echinospaerites*, with the species *E.* (i. e. *Heliocrinites*) *balticus* EICHWALD along with several Echinoidea joins the "Fam. Echini" (op. cit., p. 231). One year later, PANDER (1830, p. 143) wrote about the matter: "So wie also die Encriniten nichts anders als festsitzende, auf Stielen getragene Eurialen darstellen (CUVIER. Regne animal. Tom. IV. pag. 12), so sind die Echinospaeriten festsitzende gestielte Echini." On p. 5 it was also mentioned that HISINGER (1828, p. 195) removed these forms from the "Echinites" proper and brought them nearer to the Crinoidea. Yet certain species were interpreted as transitory forms (HISINGER 1831, p. 125). Also according to WAHLENBERG (1821, p. 52) the Hydrophoridae are intermediate between Echinoidea and Crinoidea, which was also the point of view of MEYER (1828) as appears already from the name "*Echino-Encrinites*" given to the form described by that author.

The ascription of the cystoids to the Echinoidea can readily be understood as for Swedish scientists of older times, if we keep in mind that they had before them globular bodies with numerous small plates and no or feebly developed stems, *Echinospaerites aurantium* and *Sphaeronites pomum* being by far the commonest among Swedish cystoids. Further it is quite natural that the pores were mistaken for ambulacral pores. It is equally intelligible that writers dealing with forms, the theca of which is composed by a limited number of relatively large plates and provided with a well-developed stem, should be disposed to consider their subjects as belonging to the Crinoidea. Cystoidea were put under this heading i. a. by SAY 1825, VERNEUIL 1844 (see BUCH 1844) and 1845, VOLBORTH 1845 and 1846, ROEMER 1852 and 1852—54, J. MÜLLER 1854, and by ANGELIN 1878 a, whose 'Iconographia crinoideorum' comprises two sections, viz. "Crinoidea propria" and "Cystidea". ZITTEL 1879 divided his class Crinoidea into three orders: Eucrinoidea, Cystoidea, and Blastoidea. As late as 1894 MILLER & GURLEY (p. 5) gave Cystoidea (i. e. Hydrophoridae) as an order of class Crinoidea.

The Cystoidea were first recognized as a group of their own by BUCH (1846),<sup>3</sup> who had already in 1840 communicated some observations of

<sup>3</sup> BUCH's classical paper 'Über Cystideen' is contained in 'Abhandlungen der königlichen Akademie der Wissenschaften zu Berlin. Aus dem Jahre 1844'. It should be noted that this volume was published in 1846, since the year of publication of BUCH's memoir is often quoted erroneously. An abstract in English was delivered in 'The Quarterly Jour-



“Sphaeroniten”, in which attention was paid to the merits of Swedish authors on this topic. In its original wording the diagnosis runs as follows: —

“Cystideen sind natürliche Körper, die auf einem Stiel sitzen, der sie am Boden befestigt. Ihre mehr oder weniger kugelförmige Oberfläche wird von einer grossen Menge von ineinandergreifenden polyedrischen Täfelchen oder Asseln bedeckt. Zwischen diesen Täfelchen zeigen sich die zum Leben des Thieres nothwendigen Öffnungen, unter denen sich jedoch keine befinden, aus welchen Arme, denen der Crinoideen ähnlich, hervortreten könnten. Das Thier ist völlig armlos”. (BUCH 1846 a, p. 101). — An English version was submitted in the same year (BUCH 1846 c, p. 29).

The salient point of BUCH’s diagnosis of the Cystoidea was the proposed total lack of exothecal subvective appendages. By this feature they would be separated from the Crinoidea. The actual presence of such appendages (i.e. brachioles) had been proved, however, a few years earlier by the sharp-sighted observer VOLBORTH (1842, column 298; 1845; in the first-mentioned paper called tentacles, in the second called arms) and was emphasized after the publication of BUCH’s investigations (VOLBORTH 1846, p. 161 seq.). Interpreting the brachioles as brachia VOLBORTH was unfortunately misled to classify the cystoids as true Crinoidea.

BUCH’s conception of the Cystoidea — so deserving as it was — suffered from certain shortcomings in other respects, too, which, owing to the great authority of the eminent naturalist, would for a long time be repeated in literature. BUCH’s persistent denial of the presence of armlike appendages — and, in consequence, also of pinnules — in the Cystoidea, enabled him, however, to make a statement of importance concerning a point of difference in the organization of the Cystoidea compared with that of the advanced Crinoidea (BUCH 1846 a, p. 102): the reproductive organs, which in the latter are located in the brachia, their products maturing as a rule in the pinnules which let out the eggs by simply bursting, whereas special orifices appear for the sperm, must in the Cystoidea have been enclosed in the thecal capsule (the brachioles are non-pinnulate and have contained no extensions from the coelome).

Here we should note the fact emphasized by GISLÉN (1924, p. 222) that “there existed in the older Crinoids, between the anal opening and the mouth, a pore for the primitive gonad, to which the present axial gland corresponds”. The genital glands of the pinnules developed as processes

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nal’, 2: 1 (BUCH 1846 b), soon followed by a complete English translation (BUCH 1846 c). Objections against certain declarations by BUCH were raised by AUSTIN (1848), who turned off the statement of the excentric position of the mouth in Crinoidea and the proposition of Cystoidea as predecessors of Crinoidea, referring to the fact that true crinoids appear already in Ordovician strata, i.e. contemporaneously with the cystoids then known to science.

from the organ mentioned and lost their connexion with it only at a later stage. "We may therefore suppose that the ventral sac enclosed, besides a part of the intestine, at least a part of the gonad" (l. c.). In some few forms still living the gonads mature in the arms and thus do not reach the pinnules.

The value of BUCH's statement was fully appreciated by MÜLLER (1854, p. 178), who also called in question whether BUCH's interpretation of the pyramid-bearing opening, almost regularly present in all Hydrophoridae, be correct. This conspicuous organ was maintained by BUCH to represent the "Ovarialöffnung" of the endothecal ovaries, whereas in reality it is the anal opening.

At his investigation of larval stages of *Antedon*, WYVILLE THOMSON (1865, p. 540) found the skeleton of the Pentacrinoid to be composed of two systems of plates, "the radial and the perisomatic system, thoroughly distinct in their structure and mode of growth", the former including the columnals, the centrodorsal, the radials, the brachials, and the pinnulars, the latter including the basals, the deltoids, the anals, the interradians, and any other plates of the calyx or the tegmen. THOMSON believed that "all the modifications of the skeleton which characterize the principal divisions of the Echinoderm subkingdom will be found to depend mainly upon the relative development or suppression of the radial and perisomatic systems of plates" (op. cit., p. 541). BILLINGS (1871, p. 142 seq.) applied this idea to the Cystoidea, but would prefer to consider the stem an appendage of the perisomatic system. He thought it to be safe that the Hydrophoridae do not have any radial elements in their theca but for in a small area around the mouth, a condition of things which he — in accordance with the biogenetic law formulated by HAECKEL shortly before — found to be corroborated by THOMSON's observation that "the Pentacrinoid is, at first, while yet included within the pseudembryo and during its earliest fixed stage, surrounded and enclosed by plates of the perisomatic system alone" (THOMSON 1865, p. 541). Also the theca of the blastoid genus *Pentremites* proved to be composed chiefly of plates belonging to the perisomatic system (BILLINGS 1871, p. 146). It is evident that the degree of development of each of the two named systems varies in the different classes of Pelmatozoa. But the significance of this relation for the classification is surely diminished by the fact pointed out by BATHER (1900, p. 29) that the structural character of the different plates is too vague to be used in distinguishing the skeletal elements from each other. To this must be added that the terms "perisome" and "perisomic" have varying meanings in the writings of different authors. By LOVÉN the term "perisome" was used in the more proper sense of "the general envelope"; the interradians are "the portions of it that are exposed to view between the ambulacra and outside the calycinal system" (1883, p. 10). As constituents of the calycinal system were understood the

infrabasals, the basals, and the radials (1883, p. 63). The perisome was said (1883, p. 10) to make up the whole theca of certain Hydrophoridae, e. g. *Callocystites*. In a figure of *Callocystites jewetti* HALL the perisome is beautifully shown "to be continuous under the ambulacra, which are attached solely by their first adoral plates, but otherwise free".<sup>4</sup> Further LOVÉN declared that every trace of a calyx is wanting "in the Hydrophoridae, at least in the adult". In his valuable critical paper on the morphology of the Hydrophoridae P. H. CARPENTER (1891, p. 17) denied the general bearing of LOVÉN's statement, though he found it applicable to *Sphaeronites*, *Glyptosphaerites*, and similar forms. But for many others (*Hemicosmites*, *Caryocrinites*, *Echinoencrinites*) CARPENTER was anxious to emphasize that, according to his opinion, they possess a calycinal system very much of the same type as that of the crinoids. — In WACHSMUTH & SPRINGER's paper on the perisomic plates of the crinoids (1890), which foremost deals with the homologies of the plates of the ventral surface, the reader is largely left in doubt of the meaning of the term perisomic. It seems to refer to "the small, irregular pieces [of the 'ventral pavement'] of later and recent Crinoids" (op. cit., p. 345). The same authors gave later ('The North American Crinoidea Camerata', 1897) the following definition, quoted from BATHER 1898, p. 321: — "The term perisomic plates is given to all plates which are originally developed from simple, cribriform films of limestone. They comprise the inter-radials and interaxillaries, the anals, and all ambulacral and interambulacral plates." BATHER remarked that this definition is insufficient, since also basals, radials, deltoids, and other plates ought to be comprised, though it is doubtful whether this was the intention of the authors. The term being "apparently incapable of strict definition, and corresponding to no morphological idea", BATHER (op. cit., p. 322) recommended to bury it for good, adding sarcastically that this mighty monograph by WACHSMUTH & SPRINGER afforded a fitting mausoleum.

Following JAEKEL (1918) the present author has found it appropriate to include the Blastoidea as a subclass of the Cystoidea.<sup>5</sup> For even though forming a relatively closed group, the Blastoidea do not diverge from the Cystoidea in a restricted sense (i. e. the Hydrophoridae) in any fundamental

<sup>4</sup> According to JAEKEL 1899 (p. 75) it was not recognized clearly by previous authors that the theca of the Hydrophoridae — contrary to that of the Edrioasteroidea — forms an enclosed capsule, which is not interrupted by the ambulacrals, as is evident e.g. from the Callocystitidae. JAEKEL obviously was not aware of the fact that this had been demonstrated very clearly by LOVÉN several years before.

<sup>5</sup> An arrangement in principle the same is to be found in the text-book of STROMER v. REICHENBACH (1909, p. 124), where the Blastoidea were taken as an order of the subclass Cystoidea. As further orders of this subclass were mentioned "Hydrophorida", Carpoidea, and Thecoidea (=Edrioasteroidea). As for the two last-mentioned, the present author cannot agree.



respects. It is true that the arrangement of the plates in the theca of the blastoids is strictly quinquerradiate, just as in the Crinoidea, whereas the thecal elements of the Hydrophoridae often are not affected by any very obvious symmetry whatever.

Two features common to the Blastoidea and the Hydrophoridae may be especially mentioned, namely the presence of pores piercing the thecal skeleton — hydrospires in the Blastoidea (not definitely established in the order Coronata, cf. below) and diplopores or pore-rhombs in the Hydrophoridae — having rendered it possible for the coelomic fluid to come into osmotic connexion with the surrounding medium (cf. BATHER 1919, p. 113), and the presence of biserial brachioles.<sup>6</sup>

Thecal pores of the type of hydrospires, diplopores, or pore-rhombs are regarded here as an essential cystoid character, present in no other class of the Pelmatozoa.<sup>7</sup> The taxonomic importance of these structures was, however, strongly objected to by HAECKEL (1896, p. 19 seq.) but was fully appreciated by JAEKEL, who stated that the development of pores in the Cystoidea is “gerade die wichtigste und systematisch entscheidende Eigenschaft dieser Klasse, sodass bei dem Wechsel der übrigen Eigenschaften diese schliesslich die letzte und einzige Kluft bildete, welche die Cystoideen principiell von den übrigen Pelmatozoen unterscheidet” (JAEKEL 1899, p. 172; cf. also *ibid.* p. 104 and JAEKEL 1895, p. 15 seq.). JAEKEL consequently discharged from the Cystoidea the Aporitidae of ZITTEL 1879 and several subsequent authors. The forms referred to this heterogeneous group have now been placed within the Eocrinoidea, the Carpoidea, and the Edrioasteroidea. A restricted order Aporita, with the one family Cryptocrinidae, was

<sup>6</sup> A surprising discrepancy from the ordinary development of the exothecal skeletal appendages of Hydrophoridae was made known by FOERSTE (1916 a), who described pinnulate free arms of *Caryocrinites ornatus* SAY (and *Comarocystites* which is here referred to the Paracrinoidea). In an addendum (*op. cit.*, p. 110) FOERSTE, after stating the biserial arrangement of both brachials and pinnulars, made the following remarks, however: — “Since typical crinoidal pinnules should present only a single row of pinnulars, it might be emphasized that these so-called pinnules of *Caryocrinites* are not homologous to the pinnules of crinoids, but to the brachioles of cystids.”

<sup>7</sup> In recent Crinoidea the water-vascular system is supplied with water by tegmental pores, which are thus in a way — though replacing the stone-canal — concerned with a function similar to that of the thecal pores of the cystoids, as the ambulacral system combines respiratory and hydraulic functions. — In the Ordovician crinoid genus *Porocrinus* BILLINGS pore-folds are present, which do not, however, as in Rhombifera and Blastoidea, pass at right angles across the middle of the sutures, but are located at the angles of the calycinal plates (BATHER 1900, p. 172); cf. p. 26, foot-note 10.

Certain Paracrinoidea have a subepithecal pore system, and pores may occur in certain Edrioasteroidea.

The generally accepted homology between the pore-rhombs of the Rhombifera and the hydrospires of the Blastoidea was proposed by BILLINGS (1870, p. 257).

maintained by BATHER (1900, pp. 69—70). Further BATHER's emended diagnosis of the order Rhombifera accords a place to certain forms without pores, which were reckoned there already by ZITTEL 1879. This will appear from the following quotation from BATHER (1913, p. 426, § 261): — "Stereom and stroma in folds (rhomb-ridges) at right angles to the sutures of the thecal plates, which folds are specialised as pectinirhombs in higher forms." The same was said word for word, or almost so, by BATHER 1906 (p.14), 1900 (p. 52), and 1899 (p. 919). BASSLER 1938 assumed in the main the Rhombifera as conceived by BATHER, but included also the Cryptocrinitidae, which might belong to the Eocrinoidea as well as the Macrocystellidae (this family was referred to the Rhombifera also by THORAL 1935 b, p. 110). Of the members of the original order Rhombifera, *Comarocystites* BILLINGS is here referred to the Paracrinoidea. The position of *Achradocystites* VOLBORTH and the Malocystitidae (by BASSLER 1938 referred to the Amphoridea) is doubtful. Possibly do they belong to the Paracrinoidea. *Rhombifera* BARRANDE and, with hesitation, *Tiaracrinus* SCHULTZE are to be found in the Dichoporida (= Rhombifera) of JAEKEL 1918 (p. 99), whereas they were placed among the crinoid suborder Inadunata Larviformia by BASSLER 1938. As might have appeared from the preceding, BATHER did not look upon the presence of thecal pores as an essential feature of cystoid morphology, nor were ETHERIDGE & CARPENTER (1886, p. 118) quite sure of its exclusiveness for the Blastoidea and Hydrophoridae, whereas e. g. WACHSMUTH & SPRINGER (1886, p. 125) discharged *Hybocystites* from the Hydrophoridae on account of its having neither "calicine pores, nor pectinated rhombs". And the opinion here entertained is also supported by declarations in recent publications, e. g. by FOERSTE 1938 (p. 212), who stated the new genus *Lepidocystis*, provisionally placed within the Eocrinoidea, to differ "from the Cystoidea in the absence of thecal pores", and by HECKER 1940 (p. 71) in discussing the taxonomy of the eocrinoid *Bockia* HECKER. This genus was said to have many characters in common with the Hydrophoridae. "Dagegen fehlt ein sehr wichtiges Cystoideenmerkmal — nämlich die Thekalporen; das Fehlen derselben bildet dafür ein wichtiges Merkmal der Crinoideen" (l.c.). The same statement was made about the carpoid genus *Rhipidocystis* JAEKEL: — "The main feature distinguishing *Rhipidocystis* from Cystoids is the absence of thecal pores" (HECKER 1938, p. 423). Concerning *Cryptocrinites*, JAKOVLEV 1928 (p. 373) declared that "Les trois couronnes du calice et l'absence de pores nous obligent à le ranger dans les crinoïdes".

There is undoubtedly a correlation between the lack of thecal pores with connected respiratory folds and the development of brachia in the Crinoidea, in which the thin-walled projections from the hydraulic system bordering the ambulacral grooves served for the respiration, possibly sup-

ported by respiration per anum. For pelmatozoans devoid of both thecal pores and brachia (Eocrinoidea, Carpoidea, Edrioasteroidea) we have to assume that anal respiration has played an important role, water having been sucked in and expelled again through the anus in the same way as in the recent holothurians, echinoids, and comatulids; in the last-mentioned there is a rhythmic opening and shutting of the anus, suggesting respiratory movements (cf. JAEKEL 1918, p. 114; BATHER 1928 b, p. LXXXII, JAKOVLEV 1928, p. 373; GISLÉN 1930, p. 212; GISLÉN 1934, p. 16; DEHM 1934, p. 29. Cf. also p. 46, foot-note 27 below concerning proposed "respiratory pouches" in *Cothurnocystis*).

The non-pinnulate, biserial brachioles are peculiar to the Blastoidea, the Hydrophoridea, and the Eocrinoidea. Such are also met with in some Carpoidea, namely in the Digitata HECKER and the Dendrocystitidae BASSLER. As pointed out by DEHM 1934 (p. 38), there is no principal difference between the thecal processes of the Dendrocystitidae and true brachioles. Biseriality, when present in the crinoid brachium, is, on the contrary, a secondary structure, always developed from a primary uniserial state (BATHER 1900, p. 116; 1913, p. 385, § 100), which also appears from the fact that biserial brachia frequently are uniserial at the base (cf. FOERSTE 1916 a, p. 70; JAEKEL 1918, p. 23).

In the discussion of the relations between the Hydrophoridea ("Cystoidea" s. s.) and the Blastoidea, the rare genus *Cystoblastus* has been considered a key right from the original description by VOLBORTH (1870), in which it was interpreted as a crinoid holding an intermediate position between Hydrophoridea and Blastoidea. By subsequent authors *Cystoblastus* was recognized as a member of the Hydrophoridea (Rhombifera) with a certain resemblance to the Blastoidea, called forth foremost by the loss of one of the (medio-)laterals and, as was supposed, two orals,<sup>8</sup> and by the fork-pieced shape of the radials (radiolaterals), these plates being deeply incised by the ambulacra, and, further, by the depression of the radials into the lateral cycle so as to alternate with the narrow plates of this cycle (F. SCHMIDT 1874, p. 26; NEUMAYR 1889, p. 428; CARPENTER 1891, p. 5; HAECKEL 1896, p. 131). The most penetrating morphological analysis we owe to JAEKEL, who on several occasions endeavoured to show that there is a direct phylogenetic connexion between *Cystoblastus* and the Blastoidea (1895, p. 117; 1896, pp. 690—691; 1899, pp. 158, 222 seq.; 1918, pp. 105—107). He paid special attention to the atrophy of the pore-rhombs in the laterals and their location along the ambulacra, "eine Tendenz, die in der Porenentwicklung der Blastoideen einen Abschluss findet" (JAEKEL 1899, pp. 225—226). Also the development of the respiratory folds was

<sup>8</sup> According to ETHERIDGE & CARPENTER 1886 (p. 120) *Asteroblastus* has five orals.



said to have affinity to that of corresponding elements of the blastoids. The peculiar organization of the thecal skeleton and the pore-system caused JAEKEL to look upon *Cystoblastus* as an ancestor of the Blastoidea, being a link between this group and *Cheirocrinus*. It was referred to a family of its own within the Rhombifera at the same time as it was presented as "Vorform" of the Blastoidea (JAEKEL 1918, p. 107). BATHER (1900, pp. 64—65; 1913, p. 433, § 279) placed the genus in the same family as *Cheirocrinus*, in accordance with his quite different interpretation of its morphologic features, declaring the resemblance to the Blastoidea to be purely homoplastic. Through new finds of *Cystoblastus*, JAKOVLEV was able to increase the knowledge of the genus in such direction as to reduce the convincing force of JAEKEL's argumentation (1926 a, 1926 c, 1930, 1931). Thus, from the study of an anomalously developed specimen of *Cystoblastus kokeni* JAEKEL, JAKOVLEV (1926 a) drew the conclusion that the atrophy of the pore-rhombs supposed by JAEKEL is less pronounced, the pore-line at each side of the ambulacrals representing not a quarter but a half of a primary pore-rhomb. Also the great number of actually existing pores in the lines, very much exceeding the number of pores of any other known form does not support the theory of an extensive atrophy. In the paper of 1926 c, JAKOVLEV could show that the pore-folds of *Cystoblastus* belong to the ordinary hydrophorid type and do not represent a transitory stage to the folds of the blastoid hydrospires. On the other hand it may be mentioned that ALICE E. WILSON (1932, p. 387) observed a broken rhomb plate of *Pleurocystites filitextus* BILLINGS, in which the folds were seen to continue into the cavity of the theca, indicating — according to the authoress — the relationship between the ambulacral system of the Blastoidea and this type of Hydrophoridae. — In 1931 JAKOVLEV proposed the number of orals to be five instead of three, as JAEKEL assumed.

F. SCHMIDT's article 'Ueber untersilurische Cystideen aus unserm Gebiet, die als Uebergangsglieder zu den Blastoiden gedeutet worden sind', embodied in his paper of 1874, turned the attention to some more, interesting genera, viz. *Blastoidocrinus* BILLINGS 1859, *Asteroblastus* EICHWALD 1862, and *Mesocystis* BATHER 1898 ("*Mesites*" HOFFMAN 1866). The species from the Baltic provinces described under the name of *Blastoidocrinus* were separated by JAEKEL (1918, p. 106) from the Canadian form and referred to a distinct genus, *Blastocystis*.

*Blastoidocrinus* was described in 1859 but remained insufficiently known until in 1907 HUDSON supplied further details on evidence of more perfect specimens. ZITTEL 1879 (p. 423), NEUMAYR 1889 (p. 428), &c. placed the genus in the Hydrophoridae, BATHER (1899, p. 920; 1900, p. 80) in his order Protoblastoidea, being separated from the Eublastoidea by less development of the hydrospires and a number of supernumerary plates. HUDSON

(1907, p. 119) proposed a new order, Parablastoidea, for *Blastoidocrinus*. Also *Blastocystis* might belong there (cf. below, p. 32). JAEKEL 1918 (p. 107) listed *Blastoidocrinus* and *Blastocystis* as "aberrante Versuchsformen" of the Blastoidea, "die weitere Nachfolge nicht erzielten" (op. cit., p. 106), whereas ZITTEL-BROILI 1924 (p. 222) supposed them to be true passage forms to the Eublastoidea in the same way as *Cystoblastus*. This was also the standpoint of ETHERIDGE & CARPENTER (1886, p. 120), who accepted *Blastoidocrinus* as the "only described form which appears to us to offer any real link between the Blastoids and the Crinoids or Cystids".

Like the form just spoken of, *Asteroblastus* and *Mesocystis* (and the genera *Asterocystis* HAECKEL 1896 and *Metasterocystis* JAEKEL 1918) have a certain habitual resemblance to the Blastoidea. BASSLER 1938 (p. 13) ranged them under the Protoblastoidea, in the case of *Asteroblastus* following BATHER 1899 (p. 920) and 1900 (p. 80), and SPRINGER 1913 (p. 167). These authors, on the other hand, referred *Mesocystis* to the Diplorita. With regard to the typical diplopores present in the interambulacral plates it seems well justified, however, to refer all the genera in question to the Diploporita, as did JAEKEL (1918, p. 101), ZITTEL-BROILI (1924, p. 222), and others.

Finally a few words may be said about the genera *Proteroblastus* JAEKEL 1895, *Codaster* MCCOY 1849, and *Hybocystites* WETHERBY 1880, which have also appeared in the discussion of the relations between Hydrophoridae and Blastoidea.

*Proteroblastus* has generally been recognized as belonging to the Diploporita, but BATHER (1900, p. 78) stated that it can hardly be distinguished from primitive Blastoidea. Now, as we have seen, most of BATHER's Protoblastoidea have to be placed in the order Diploporita of the Hydrophoridae.

*Codaster* ("Codonaster" ROEMER 1852) was discussed at some length by NEUMAYR 1889. This form, which "schon mehrfach als eine Zwischenform zwischen Cystideen und Blastoideen erwähnt, ja von manchen, wenn auch mit Unrecht, geradezu bei den ersteren eingereiht worden ist" (op. cit., p. 427),<sup>9</sup> was said to differ considerably from typical blastoids with regard to the development of the hydrospires "und zeigt in diesem einen Merkmale vollständige Uebereinstimmung mit manchen Cystideen, *Codonaster* ist geradezu eine Blastoidee mit den Röhrenbündeln (Hydrospiren) einer Cystidee, und seine Bedeutung als wichtiges Bindeglied zwischen beiden Classen steht unbestreitbar fest" (op. cit., p. 428). Most prominent students of pelmatozoa, yet excepting BILLINGS (1870, p. 263), have agreed in referring *Codaster* to the Blastoidea, but the interpretation of its position has varied. BATHER (1900,

<sup>9</sup> *Codaster* was removed from the Blastoidea by certain authors (ROFE 1865, p. 251; BILLINGS 1870, p. 263; ZITTEL 1879, p. 424), i.e. on account of the lack of spiracles at the end of the ambulacra and of pores along their sides.

p. 82) considered the genus the least specialized of all eublastoids, JAEKEL (1918, p. 109), on the contrary, found it to be extremely specialized with regard to pore-structure. Though superficially resembling the pore-rhombs of the Rhombifera, the development of the pore-slits was demonstrated to have been a quite different one (cf. also ETHERIDGE & CARPENTER 1886, p. 264).

In 1880 A. G. WETHERBY published a paper containing the description of a peculiar pelmatozoan, called *Hybocystites*, from the Trenton of Kentucky. The generic name was chosen to indicate how this "genus combines, in a remarkable degree, characters both of the Crinoids [*Hybocrinus* BILLINGS] and Cystids" (p. 150). WETHERBY "referred it to the Cystidae with some hesitation, but mainly on account of the anomalous arrangement of the ambulacral system, three rays of which are upright and two oppressed" (p. 152). CARPENTER (1882, p. 309) did not believe that this form possesses any brachia, but interpreted the supposed "arms" as "upward prolongations of the radials" (loc. cit.). As for the two "oppressed ambulacra", CARPENTER was inclined to find them equally comparable to the ambulacra of the blastoids and, consequently, the relations of *Hybocystites* to be rather with this group and the crinoids than with the cystoids. But he refrained from fixing its systematic position. The affinity to the blastoids proposed by CARPENTER was modified by ETHERIDGE & CARPENTER (1886, p. 120), who stated that *Hybocystites* is "in some respects — very like a Blastoid, but the resemblance is more a superficial than a fundamental one". NEUMAYR (1889, p. 438) remained on the standpoint of CARPENTER 1882. The pentamerous base, the uniserial brachia, &c. indicate clearly that *Hybocystites* is a true crinoid, and as such it has also been looked upon by subsequent writers. WACHSMUTH & SPRINGER 1886 took it »to be a Palaeocrinoid of low organization" (p. 124) and thought "like WETHERBY that the ambulacra resemble decidedly those of the Cystids, and not those of the Blastoids" (p. 125). The Hybocrinidae, to which *Hybocystites* belongs, were placed at the base of the Inadunata by BATHER (1900, p. 144) "because of their simple structure and resemblance to Eublastoidea".

By the above examples the present author has endeavoured to demonstrate how, at different times, distinguished investigators of Pelmatozoa have felt the limit between Hydrophoridae and Blastoidea to be in flux. So it was in fact no very revolutionary measure when, in 1918, JAEKEL ranged the Blastoidea as a subdivision of the Cystoidea. And among expressions of deviating opinions we also find declarations which anticipate JAEKEL's arrangement, though for formal or other reasons the authors in question hesitated to go the whole length. WACHSMUTH & SPRINGER 1886 (p. 206), in discussing the Stephanocrinidae, found it inappropriate to make not only the Hydrophoridae and Blastoidea but also the Crinoidea distinct classes.



Within the earlier portion of their joint work on Blastoidea, ETHERIDGE & CARPENTER (1886) saw the affinity to the Hydrophoridea so as to express their doubt "whether the Blastoids and Cystids are in reality sufficiently distinct to rank as separate classes" (op. cit., p. 4). But later they quitted this point of view and were "led to the conclusion that the group Blastoidea is in reality an extremely well defined one, and that there is perhaps a closer affinity between Cystids and Crinoids through *Porocrinus* than between the former group and the Blastoids, no really intermediate type being known to us" (op. cit., p. 117).<sup>10</sup> BATHER was fully aware of the connexion between Hydrophoridea and Blastoidea and gave voice at several occasions to his conviction in this respect. Thus in 1899 (p. 918): — "The Diploporita, however, tend gradually and clearly in this direction [i.e. towards completely correlated symmetry in the theca], and lead imperceptibly to the Blastoidea. Either the Blastoidea, as hitherto understood, must be placed with the Cystidea, or their limits must be enlarged to include such Diploporita as have this definite correlation and plates that can be called 'radials'. The latter course enables us to define the Cystidea with greater precision, and is therefore adopted." And in 1900: — "The Diploporite line ought properly to include the Blastoidea" (p. 39), and further (p. 43): — "The Diploporita — — — show a gradually increasing regularity of structure in the food-grooves, and in their relations to the theca, leading almost imperceptibly to the Blastoidea. So much is this the case that it seems well to separate from the Cystidea certain forms in which 'the radial polymeric symmetry' is 'in complete correlation with the radial symmetry of the ambulacra' — —, and to refer them to the Blastoids as an order Protoblastoidea — —. The only alternative is to make the Blastoids an order of the Cystidea." The last time BATHER wrote about the system of the Pelmatozoa was in an article in 'The Encyclopedia Britannica' (1929 a). Here he stated that "the Blastoidea, though numerous and rather sharply defined, are a relatively late off-shoot from the Cystoidea, and if they are retained here as a class, it is only because authorities disagree upon their point of origin" (op. cit., p. 898).

At the end of this discussion concerning the interrelations of Hydrophoridea and Blastoidea, it should be emphasized that the existence, or the non-existence, of true intermediate types is, strictly, not relevant to the solution of the question. To be sure, every scientist who has dealt systematically with a material, extensive enough, of any group of recent organisms, has often had to examine his conscience before the task of setting apart

<sup>10</sup> *Porocrinus* BILLINGS, from the Ordovician and Lower Silurian of Canada, Kentucky, and USSR, is a true crinoid, belonging to the Inadunata-Fistulata. The calycinal plates are furnished at the angles with deep folds, which do not, however, cross the sutures. These so-called goniospires were mistaken for pore-rhombs by several authors, and on account of that *Porocrinus* was referred to the Hydrophoridea.

certain doubtful forms. And yet his investigation material represents a transverse section through a line of evolution and not a more or less uninterrupted longitudinal section. The difficulties are by far more embarrassing for the paleontologist, who has to survey a fossil material collected from a series of strata, the deposition of which may have lasted for thousands and millions of years. In this space, the time-factor has acted incessantly upon the organisms and has left its impress on the generations following each other. Irrespective of the way of acting of the evolutionary process, it is a fact — brought to the memory of the paleontologist again and again — that two forms which are in themselves defined well enough, are linked together by an intermediate type, or by a series of intermediate types. Should the extremes of this morphological line be looked upon as different species (i.e. genetically conditioned links in an evolutionary chain) or the younger as a mere modification of the older one? It seems inevitable, in point of principle, to let the first-mentioned way of looking at the matter be the predominating one. If not, we will have to disqualify all taxonomic categories, for not only the conception of species but also that of each higher systematic unit is concerned to a certain extent. Thus we could not help disintegrating the systematic construction which is indispensable to science, who aims at being master of the multitude of organic beings. In this connexion the author is anxious to emphasize that, by the above reasoning, he does in no way intend to plead for a classification based on strait-laced formal-morphological considerations. The ideal classification should bring the phylogenetic continuity out but must not allow the stages — more or less persistent — of the integrate evolutionary lines to be obliterated throughout. Especially for the purpose of stratigraphy the small taxonomic units must be contained within rather narrow limits. It may be objected that the combining of these principles into one systematic construction will not be possible to achieve. But why not try to approach the ideal?

In the case of Hydrophoridae and Blastoidea, they have been ranked here as subdivisions of the class Cystoidea, less on account of their being linked together by suggested intermediate types than on account of their having in common certain essential features of organization, foremost thecal pores and biserial brachioles.

We have seen above (p. 25) how a consistent underlining of the signification of intermediate forms caused WACHSMUTH & SPRINGER (1886, p. 206) to deny the existence of a limit between the Cystoidea and the Crinoidea.<sup>11</sup> In reality the two groups differ in important respects, as we have already had occasion to point out repeatedly on the preceding pages. In addition to

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<sup>11</sup> To take an example from a different phylum, the Chaetopoda and the Hirudinea would equally be disqualified as taxonomic units of higher rank because of the existence of *Acanthobdella*!

the features mentioned (brachia, lack of calycinal pores, rigorous polymeric symmetry), the Crinoidea are characterized i.a. by the differentiation of the corona (exclusive of the skeletal appendages) in a dorsal calyx (or patina) and a ventral tegmen, i.e. the oral surface between the bases of the brachia, which latter have moved from the immediate vicinity of the mouth. The anus is usually located to the tegmen. A similar differentiation is visible in *Caryocrinites* but otherwise not typical of the cystoids.

The relation between Hydrophoridae and Crinoidea as interpreted by certain older paleontologists was already touched upon above (p. 16).

### Subclass Hydrophoridae.

In BASSLER's index (1938) the class Cystoidea (i.e. the Pelmatozoa exclusive of the Blastoidea and Crinoidea) was divided into the orders Amphoridea, Rhombifera, Diploporita, and Edrioasteroidea. The arrangement given must be characterized as a step backwards from the point of knowledge of these organisms reached first and foremost by the investigations of JAEKEL and accepted gradually in the main also by BATHER.

The grounds for removing the Edrioasteroidea from the Cystoidea and ranking them as a separate class will be presented below (p. 43).

Following JAEKEL the order Amphoridea of HAECKEL, of which BATHER was for a long time an advocate until at last he changed his position, has to be split up into very different groups to be referred to the Diploporita, Paracrinoidea, Eocrinoidea, and Carpoidea. The three classes last mentioned will be discussed further below.

After removing the forms referable to either of the Paracrinoidea, Eocrinoidea, and Carpoidea, the Aristocystitidae only remain of the families listed by BASSLER (1938) as Amphoridea. JAEKEL 1899 (p. 407 seq.) and 1918 (p. 103) referred the fam. Aristocystitidae to the Diploporita and placed it close to the Sphaeronitidae. BATHER 1900 (p. 44 seq.) included it in the Amphoridea, and in 1906 (p. 7) he declared — after JAEKEL's criticism (1900) of HAECKEL's group Amphoridea had been published — that "the order Amphoridea, however much it be dismembered, still seems to find justification in the existence of genera, such as *Aristocystis*, which have neither diplopores (so far as I can observe) nor epithelial extensions of the subvective grooves, and probably other genera, such as *Calix*, in which imperfect or occasional diplopores exist, uncombined, so far as we know, with the epithelial subvective system characteristic of the Diploporita". From the scanty and rather poorly preserved material of *Aristocystites* (a few specimens from Zahořany, Bohemia) available to the present writer, it was not possible to judge whether the pores are to be interpreted as haplopores or diplopores. In a recent communication on an occurrence of



*Aristocystites* in China, SUN (1936, pp. 478, 480) spoke of the pores as "double pores".<sup>12</sup> As for the other objection raised by BATHER — the supposed lack of brachioles in the *Aristocystitidae* — it is true that any sub-ventive appendages have not been observed, but a reduced number (2—4) of brachiole facets has been stated to be present (JAEKEL 1918, p. 103; ZITTEL-BROILI 1924, p. 218; SUN 1936, p. 478, &c).

The position of the genus *Calix* ROUAULT also called attention to by BATHER 1906 is not quite clear. JAEKEL 1899 (p. 402) and, with a mark of interrogation, JAEKEL 1918 (p. 103) and ZITTEL-BROILI 1924 (p. 220) placed it in the fam. *Sphaeronitidae*. BASSLER 1938 (p. 8), on the other hand, referred it to the fam. *Aristocystitidae* of the order *Amphoridea*. It seems to be safe, however, that *Calix* belongs to the *Diploporita*, even though its closer relationship cannot be decided as yet. In a diagnosis of the genus, CHAUVEL (1936, p. 2) stated definitely that "toutes ces plaques sont traversées par des canaux diploporiques débouchant par paires au fond de fossettes diploporiques".<sup>13</sup>

We shall have to take a look at the other genera, too, referred by BASSLER 1938 to *Aristocystitidae*. Some of these are so imperfectly known that no definite opinion of their belonging can be raised. This must be said of *Aenigmatocystis* T. H. CLARK 1924, *Amphoracystis* HAECKEL 1896, *Lapillo-*

<sup>12</sup> Even though diplopores may be characteristic of typical representatives of *Aristocystites*, the very species from India closely studied by BATHER (1906) and called by him *Aristocystis dagon* differs, as confirmed SUN (1936, p. 480), "by the character of the pores (not doubled)". SUN proposed this species to be no *Aristocystites* at all but to belong to a distinct genus, *Pseudaristocystis* (cf. foot-note 13).

<sup>13</sup> CHAUVEL (1936, p. 3) pointed out that the Bohemian genus *Craterina* BARRANDE and the SW European *Calix* ROUAULT (ex parte) [which was, moreover, lately stated to be represented also in Bohemia (CHAUVEL 1939)] cannot be allowed to be identified as proposed BATHER (1900, p. 46; 1919, p. 73) and, following him, BASSLER (1938, p. 57). JAEKEL (1899, 1918) took *Craterina* (under the name of *Codiacystis* JAEKEL 1899) and *Calix* as separate genera.

In a similar way as *Pseudaristocystis* SUN differs from *Aristocystites* BARRANDE, *Pachycalix* CHAUVEL 1936 differs from *Calix* by having haplopores. The present writer is not quite sure where to place the two genera mentioned, but in view of their close affinity to forms with normally developed diplopores, it might be possible that the haplopores were derived from diplopores, on account of which *Pseudaristocystis* and *Pachycalix* could be referred to the *Diploporita*.

Parenthetically may be mentioned that the Lower Devonian *Lodanella mira*, which was described by E. KAYSER in 1885 (Z. Deutsch. Geol. Gesellsch. **37**, Berlin, p. 207 seq.) as a sponge, was interpreted as a cystoid closely allied to *Calix* and *Craterina* independently and almost contemporaneously by three different authors, viz. JAEKEL 1899 (p. 404), BATHER 1900 (p. 46), and CL. SCHLÜTER 1900 (Z. Deutsch. Geol. Gesellsch. **52**, Berlin, p. 178 seq.). Later, by the aid of new and better material, JAEKEL (Paleontol. Z. **1**, 1914, Berlin, p. 382, seq.) succeeded to find out that *Lodanella* in reality is a crinoid, belonging to *Edriocrinidae*; this conception is now accepted generally.

*cystites* BARRANDE 1887, and *Pilocystites* BARRANDE 1887. *Baculocystites* BARRANDE 1887 belongs to the Diploporita, as far as can be inferred from BARRANDE's Pl. 36, fig. 2 a. This is also true of *Hippocystis* BATHER 1919, in which "the pores are far more obviously in pairs" (than in *Aristocystites*) (BATHER 1919, p. 72), and of *Holocystites* HALL 1864 [cf. BATHER 1919, p. 110: — "Essentially the pores of *Megacystis* (i.e. *Holocystites*) are diplo-pores"]. The last-mentioned genus was referred to the fam. Aristocystitidae, Diploporita, by JAEKEL (1899, p. 413; 1918, p. 103, under the name of *Trematocystis* JAEKEL 1899) and by ZITTEL-BROILI (1924, p. 219, under the name of *Megacystis*). *Deutocystites* BARRANDE 1887, finally, was identified with *Echinosphaerites* by JAEKEL (1899, p. 331), rightly, as thinks the present writer; the figures of *Deutocystites modestus* delivered by BARRANDE (1887, Pl. 15, case 2) are namely undoubtedly reminiscent of moulds of *Echinosphaerites*. It may be mentioned that the identification was accepted by ZITTEL-BROILI (1924, p. 214). BATHER (1906, p. 15) thought the identification an open question.

From this review it should have appeared, though there remains some doubt as to the position of a few genera, that the fam. Aristocystitidae has to be removed from the fatal Amphoridea and to be placed mainly in the Diploporita. By this procedure there is nothing to be left of the order Amphoridea in the sense of BASSLER 1938. And it is significant that the Amphoridea got no room in the last system of the Pelmatozoa published by BATHER (1929 a).

From our Hydrophoridea one more group has to be excluded, viz. the genera belonging to the families Cryptocrinitidae and Macrocystellidae, which correspond in part to the Aporitidae ZITTEL 1879. BASSLER 1938 (p. 11) referred those families to the Rhombifera. Now, as we have had occasion to emphasize repeatedly, the presence of thecal pores is one of the bearing features in cystoid organization. Therefore it would be in itself an absurdity to include the Aporitidae (or Aporita, as wrote e.g. BATHER 1900, p. 69, and BASSLER 1938, p. 11)<sup>14</sup> in any group belonging to the Cystoidea. It should be pointed out that the Aporitidae are not likely to have been derived from poriferous forms with regard to the fact that their oldest representatives appeared earlier — in the Middle Cambrian — than the Hydrophoridea. Following JAEKEL 1918 they are referred to the Eocrinoidea here, which are in the present paper interpreted as a separate class.

For the subclass Hydrophoridea thus delimited it comes natural to recognize two larger divisions based on the different development of the pores of the thecal plates. This distinction was made already by MÜLLER (1854). Thus Hydrophoridea with diplopores in the stereom, seldom travers-

<sup>14</sup> ANGELIN, in his 'Iconographia crinoideorum', used the term "Aporita" in a special sense (cf. below).

ing the sutures of plates and often restricted to definite tracts or plates, are contained in the order *Diploporita* J. MÜLLER 1854, emend. BATHER 1906. The second division, the order *Rhombifera* ZITTEL 1879, emend. BATHER 1899 (this conception is covered almost in detail by the term *Dichoporita* JAEKEL 1899), receives *Hydrophoridae*, the stereom of which is provided with tubular pores common to two adjacent plates and traversing the sutures of plates at right angles. The two orders, which are of course separated by several other characters too, have been so well founded and discussed, especially by BATHER and JAEKEL that there is no need here to dwell upon the matter. These orders are now generally accepted.

Finally, just a few words will be said of the classification used by ANGELIN (1878 a) in his 'Iconographia crinoideorum'. The genera dealt with were referred to one of the following divisions: — "Apora", "Gemellipora", and "Pedicellata; Rhombifera". The first-mentioned group, the "Apora", is not quite easy to understand. It comprises "*Echinosphaera*", the heterogeneous "*Caryocystis*", and "*Megacystis*". Obviously it is not identical with the *Aporitidae* of subsequent authors. For *Echinosphaerites*, JAEKEL (1899, p. 108) undoubtedly correctly, gave the explanation that in well-preserved specimens the pores are not directly visible, being covered by a smooth epithek. As to *Caryocystites*, *Heliocrinites*, &c. ("*Caryocystis*" of ANGELIN), ANGELIN cannot have detected the real character of the pore-rhombs, otherwise they would not have been designated as aporous. The second group, the "Gemellipora" (from Lat. *gemellus*, twin) corresponds to the *Diploporita*, whereas the third group, the "Pedicellata; Rhombifera" (from Lat. *pedicellus*, small stalk) is very arbitrary; it contains two genera only: *Cheirocrinus* ("*Glyptocystis*"), and *Lovénicystis* n.g. ("*Lepadocrinus*").

Stratigraphic range: — Middle Ordovician—Middle Devonian.

### Subclass Blastoidea.

The dividing into orders of the subclass Blastoidea will be dealt with rather summarily, only to state the reason for the arrangement here adopted, which differs in certain not unimportant respects from that of BATHER (1899, 1900) and BASSLER (1938), and does not coincide fully with that of JAEKEL (1918).

The first more extensive treatise on Blastoidea was written by ROEMER (1852). All species described by ROEMER were referred to three genera only, all of them belonging to the order Eublastoidea BATHER [*"Pentatremites"* SOWERBY 1828 (= *Pentremites* SAY 1820), "*Elaeocrinus*" ROEMER 1852 (= *Nucleocrinus* CONRAD 1842), and "*Codonaster*" ROEMER 1852 (*Codaster* MCCOY 1849)]. No dividing into higher taxonomic categories was undertaken.

ETHERIDGE & CARPENTER, in their monograph of 1886, recognized two



orders, Regulares and Irregulares, of their class Blastoida, which corresponds to the Eublastoida only. There is no reason to enter here upon a discussion of the subdividing of the Eublastoida, but it may be mentioned that the two sections proposed by ETHERIDGE & CARPENTER were declined by BATHER (1899, p. 918; 1900, p. 91), who found them to be based on variable characters. Yet they were maintained by ZITTEL-BROILI 1924.

In 1899 BATHER divided the Blastoida into two "grades", Protoblastoida and Eublastoida, on grounds which were further explained in 1900. Eublastoida comprises forms, the thecal plates of which "have assumed a definite number and position in three circlets". Interambulacral folds, running across the radio-oral sutures, "hang down into the thecal cavity, forming the hydrospires" (BATHER 1900, p. 81). The order Radiolata of JAEKEL (1918) is equivalent to this section, which is made up of the bulk of the blastoids, and corresponds to the class Blastoida of authors.

The second "grade" established by BATHER, the Protoblastoida, was quite dismembered as the knowledge of the heterogeneous forms referred there increased. BATHER's diagnosis (1899, p. 920; 1900, p. 79), excluded forms with hydrospires.<sup>15</sup> So *Blastoidocrinus* had to be removed and was placed by G. H. HUDSON (1907, p. 119) in the order Parablastoida, to which also *Blastocystis* JAEKEL might belong.

It was already mentioned above (p. 24) that *Asteroblastus*, *Asterocystis*, *Metasterocystis*, and *Mesocystis*, referred by BASSLER 1938 (p. 13) to the Asteroblastidae, are true Hydrophoridae Diploporita. Of the Protoblastoida listed by BASSLER 1938 thus only *Paracystis* SJÖBERG 1915 remains. BASSLER referred this genus with hesitation to the Asteroblastidae, to which it does not belong, however, i.a. on account of the lack of diplopores. The taxonomic position of *Paracystis* is yet somewhat doubtful. It is joined here tentatively with *Stephanocrinus* CONRAD 1842, *Mespilocystites* BARRANDE 1887, emend. JAEKEL 1927, *Stephanoblastus* JAEKEL 1918, and *Tormoblastus* JAEKEL 1927, forming the order Coronata JAEKEL. The small size of the theca and the not very well defined sutures of the plates make an analysis of the arrangement of the thecal plates of *Paracystis* rather difficult. Accord-

<sup>15</sup> BATHER's diagnosis of 1899 states categorically: — "no hydrospires". The diagnosis of 1900 runs as follows: — "Blastoida without interambulacral groups of hydrospire-folds hanging into the thecal cavity", which must mean, de facto, that no hydrospires are allowed to be present, since folds dipping into the thecal cavity are the very constituents of hydrospires. So it is surprising that BATHER ranged *Blastoidocrinus* with the Protoblastoida in spite of "incipient hydrospires" (BATHER 1900, p. 80) being recognized in the genus. Its affinity to the Eublastoida was also pointed out, being separated by no other character "than the less development of the hydrospires" (op. cit., p. 81). SPRINGER (1913, p. 167) did not take the lack of hydrospires as a character of the order Protoblastoida but only of its family Asteroblastidae. Order Protoblastoida in the emended sense of SPRINGER's is therefore equivalent to Parablastoida HUDSON.

ing to the opinion of the present writer, the interpretation given by SJÖBERG (1915) is in no way correct, certain ridges on the surface of the skeleton plates having been mistaken for sutures and the obscure true sutures not having been observed. The genus will be further dealt with below.

JAEKEL's order Coronata has not been left unmolested either. W. E. SCHMIDT (1923, p. 152) characterized it as "eine ganz zweifelhafte Gruppe". In 1924 WANNER raised objections against the retaining of the Coronata in a discussion of the dividing of the Blastoidea, which, however, does not seem to have been performed quite logically. On the one hand he vindicated (WANNER 1924, p. 4) the opinion that JAEKEL's orders Radiolata and Coronata might be dropped, the former being coincident with Eublastoidea BATHER, which is correct, the latter being no typical blastoids ("*Eublastoidea* im Sinne BATHERS"), which they were, however, not proposed by JAEKEL to be. According to WANNER, the Coronata are destitute of lancet-plates and hydrospires, characteristic of the Blastoidea, whereas their positive characteristics — high interrarial prolongations of radialia between the ambulacra, the mouth being immersed and surrounded by orals, and the location of the brachioles at the end-points of the ambulacra — are not confined to this group but met with also in typical blastoids, viz. the genus *Timoroblastus* WANNER,<sup>16</sup> which was said to join the features mentioned of the Coronata with the lancet-plates and hydrospires of Eublastoidea. On the other hand, WANNER (1924, p. 4) pointed out that *Mespilocystites* BARRANDE, *Stephanoblastus* JAEKEL, and *Stephanocrinus* CONRAD, the only genera of Coronata then known, might possibly be congeneric, and *Stephanocrinus* was referred to the Blastoidea: "In der Auffassung der Gattung *Stephanocrinus* CONR. freue ich mich JAEKEL zustimmen zu können, soweit deren Zugehörigkeit zu den Blastoiden in Betracht kommt." Yet he expressed doubt whether *Stephanocrinus*, forming the order Coronata, could stand opposed to all other Blastoidea.

WACHSMUTH & SPRINGER (1886, p. 206 seq.) discussed the systematic position of *Stephanocrinus* at some length. They arrived at the conclusion that it "agrees by its oral and anal pyramid with certain forms of the Cystids, while in its general habitus and in the position of the ambulacra it agrees with the Blastoids; and yet it is, as we shall prove, unquestionably a Palaeocrinoid". Of crucial importance for their point of view was the supposed possession of "branching biserial arms, given off in a somewhat similar manner as the arms in the Platycrinidae" (WACHSMUTH & SPRINGER 1886, p. 208). BATHER (1900) accepted this observation and declared that *Stephanocrinus* "undoubtedly belongs to the simplest and most primitive group of

<sup>16</sup> In *Timoroblastus* the interrarial prolongations are made up exclusively of the oralia, whereas in *Stephanocrinus* the radialia also take part in their formation (cf. WANNER 1924, p. 16).

the Crinoidea, and it is hard to believe that its remarkable resemblances to Eublastoidea are merely homoplastic, especially since the position of the small basal is not one which usually occurs in other Crinoidea that have fused basals" (p. 97). He admitted that the plates are arranged as in Eublastoidea, that certain interrarial pits between the deltoids and adjacent radial processes may be atrophied hydrospires, and that the ornament of the plates is strongly reminiscent of that in Eublastoidea. ETHERIDGE & CARPENTER (1886),<sup>17</sup> SPRINGER (1913, p. 207), ZITTEL-BROILI (1924, p. 177), also referred *Stephanoblastus* to the Crinoidea but pointed out its close relationship to the Blastoidea. The latest record of Paleozoic pelmatozoans, that of BASSLER 1938, which is largely based upon the works of BATHER, listed *Stephanocrinus* among Inadunata Larviformia.

The first to make *Stephanocrinus* the subject of a special investigation, ROEMER in 1851, (and later some other authors) looked upon it as a cystoid (i.e. a hydrophorid). Still many years later ROEMER (1887, p. 196) repeated his statement. But this view is not tenable, i.e. on account of the lack of diplopores or pore-rhombs.

ZITTEL 1879 (p. 436) with hesitation referred the genus to the Blastoidea, whereas S. A. MILLER 1889 expressed a positive opinion as to its belonging there, thus being a predecessor of JAEKEL and WANNER, as we have seen. The last-mentioned student (WANNER 1924, pp. 16—17) succeeded to shed light upon certain previously doubtful features of organization in *Stephanocrinus*, foremost by comparison with the Permian blastoid genus *Timoroblastus* from Timor. The arguments presented by JAEKEL in 1918 for the blastoid nature of *Stephanocrinus* and its belonging to a separate order, were set forth again in a paper on *Tormoblastus*, a related genus from the so-called Leptaena limestone of Dalarna, Sweden (JAEKEL 1927 a). With regard to the following features of organization *Stephanocrinus* and its allies proved to be true blastoids: development and arrangement of the skeleton elements throughout blastoidean; radiomerous construction of the ambulacra; exothecal subvective appendages delicate, biserial, and evidently non-pinnulate, i.e. brachioles. The imagination that the appendages were branching may be due to the fact that they are concentrated to the distal end-point of each ambulacrum. In this respect they differ from typical Blastoidea, in which the brachioles are arranged in two rows all over the ambulacra. JAEKEL (1927 a, p. 3) presumed that this divergence may be put in connexion with

<sup>17</sup> Some discrepancies in their text are due to the fact that the authors, when beginning their work, considered *Stephanocrinus* a blastoid ["it was not till March last that we learnt of Mr. WACHSMUTH's most important discovery that *Stephanocrinus* is not a Blastoid at all, but a Brachiate Crinoid. The earlier sheets of this work, therefore, contain many passages which would have been differently expressed had we known as much when they were written as we do now" (ETHERIDGE & CARPENTER 1886, p. VIII)].



the peculiar interrarial prolongations of the radialia, which must have impeded the normal spread of the brachioles over the ambulacra, if their subvective function should be performed. By this, an arrangement much the same as in certain Crinoidea was effected, which can, however, not be considered so important as to be the motive of separating the Stephanocrinidae from the Blastoidea. Nor does this be true of the last objection against the blastoid nature of this group, viz. their lack of hydrospires. How this really be, is, however, not quite clear. CARPENTER (1882, p. 311) expressed it cautiously: the ambulacra of *Stephanocrinus* are "possibly devoid of hydrospires". BATHER (1900), as just mentioned, did not deny the possibility of atrophied hydrospires being traceable. The other available members of this group are not preserved well enough and (or) make observations too delicate by their minute size.

Thus, following JAEKEL (1918, 1927 a), WANNER (1924), and MOORE (1940, p. 579), we may properly classify *Stephanocrinus* as a blastoid. And, according to the opinion of the present writer, no important objections against the relationship of the forms referred by JAEKEL to Stephanocrinidae have as yet been set forth, certain features of organization though being still obscure. Further, considering the strong, or maybe entire, atrophy of the hydrospires, and the concentration of the brachioles to the distal end-points of the ambulacra, it seems to be well justified to rank the Stephanocrinidae as a paratypical order of the Blastoidea, as did JAEKEL by introducing his order Coronata.

Blastoidea existed in the time-space Middle Ordovician—Lower Permian.

### Class Eocrinoidea.

The group was defined by JAEKEL 1918 (p. 24) and ranked as a subclass of Crinoidea. Among recent authors adopting this view may be mentioned HECKER (1940, p. 68, &c.).

That it is here taken as a class is for the same reason as in the case of Paracrinoidea: the forms referred here join features from the Cystoidea on the one hand and from the Crinoidea on the other. Therefore, in the writer's opinion, it would not be appropriate to classify them either as Cystoidea or as Crinoidea. This, of course, does not mean that the present author does not recognize the close relationship and phylogenetic connexion between the Eocrinoidea and the classes mentioned, which has, maybe, been demonstrated particularly clearly by the investigation of JAKOVLEV on *Cryptocrinites* (1918, 1926 b, 1927, 1928). A comprehension of JAKOVLEV's results was given by FEDOTOV 1928 (pp. 51—52). With regard to its tricyclic theca and the lack of thecal pores, *Cryptocrinites* was referred to the Crinoi-

dea. Supernumerary plates were observed, however, in anomalous specimens, which provides "highly important data not only on the origin of *Cryptocrinus* from the Dichoporita Regularia (Cystoidea Rhombifera), but also elucidates the course and character of the evolutionary process in the given case" (JAKOVLEV 1918, p. 23). There is no reason here to go into details, it may only be said that the mode of branching of the ambulacral grooves and the location of the anus to the latero-ventral side were mentioned as other features proper to the cystoids (i.e. Hydrophoridae). Yet *Cryptocrinites* was looked upon as a true crinoid, for JAKOVLEV did not believe in transitory stages, the evolution being performed by saltatory variations. "In such variations no intermediate forms can appear, the modification taking place, when one generation is succeeded by the one, immediately following" (JAKOVLEV 1918, p. 25). "The causes which led to the diminution of the number of cycles of plates are, probably, those that determined the development of the Cystoidea into Crinoidea, i.e., first of all, the tendency to replace the pore-rhombs as respiratory organs by the development of arms" (l.c.).

HECKER (1938 a, p. 424; 1940, pp. 71—72), contrary to JAKOVLEV, emphasized the intermediate position of the Eocrinoidea, though he referred them to the Crinoidea. Yet he remarked (1938 a, p. 424) that *Bockia* HECKER 1938 "may be provisionally [spaced out by the present author] referred, along with *Cryptocrinus*, to the Crinoids — namely to their subclass Eocrinoidea".

The author has endeavoured to show above (p. 20 seq.) that the thecal pores are an essential cystoid character, altogether unfamiliar to the crinoids. Thus, because of the lack of pores, we cannot refer the Eocrinoidea to the Cystoidea but would rather place them in this respect in the neighbourhood of the Crinoidea. On the other hand, in addition to certain cystoid features just mentioned, there is a character, given in JAEKEL's diagnosis of the group (1918, p. 24), which does immediately exclude the Eocrinoidea from the crinoids, viz. the development of biserial brachioles (cf. p. 22 above). So it seems to be adequate to rank the Eocrinoidea as an independent class, in spite of the doubts as to such a step expressed by JAEKEL (1918, p. 13): — "Aus diesen Erwägungen möchte ich die Eocrinida als Unterklasse im Rahmen der Crinoiden festhalten, obwohl ein Teil ihrer Formen sich als einzelne aberrante Versuchsformen ebensoweit vom Normaltypus der Crinoiden entfernen, wie etwa die Cystoideen. Sie enthalten aber vor allem die primitivsten Vorfahren der sämtlichen Crinoiden und deshalb lassen sie sich nicht gut aus dem genetischen Verbande dieser Entwicklungsreihe herauslösen, während jene aberrante Versuchsformen ephemer und isoliert blieben und deshalb keine systematische Einheiten füllen würden." The validity of the reasoning quoted is, according to the opinion of the present author, considerably

affected and weakened by a proposal further on in the same memoir, namely that "die Carpoideen von primitiven Eocystiden — — — abstammten" (JAEKEL 1918, p. 118). In consequence, it would be equally unsuitable to disengage these groups from their genetically conditioned connexion.

As a proof of the unsafeness of the systematic position of the Eocrinoidea in relation to the true crinoids it may further be mentioned that CRONEIS & GEIS (1940, p. 347), having observed in an early larva of the blastoid genus *Mesoblastus* a certain similarity to *Cryptocrinites* in shape and in number and arrangement of the plates, put in question whether this resemblance might be significant for some genetic affinity between the blastoids and the "aporitan cystoids", i.e. the Eocrinoidea.

It may also be mentioned that in ZITTEL-BROILI's text-book (1924, p. 222) the Eocrinoidea<sup>18</sup> were appended to the Hydrophoridea. BATHER (1900, p. 69) included the Cryptocrinitidae in the order Aporita. He remarked that the "arrangement of the thecal plates, and a homoplastic resemblance to *Hypocrinus*, have suggested to some a connection with the Crinoidea".

No undisputed representatives of the Eocrinoidea being known from Sweden, there is no need in this connexion to enter upon a discussion of the subdividing of the group, performed by JAEKEL (1918, p. 24 seq.). Several genera, which had been referred to the Hydrophoridea — partly to the Amphoridea HAECKEL and partly to the Aporita ZITTEL — were classified as Eocrinoidea. Taking as a basis the latest survey of the Pelmatozoa, that of BASSLER 1938 (p. 8 seq.), which mainly follows BATHER's arrangement of 1900, it has to be modified in such a way that the following families are transferred to the Eocrinoidea: — Eocystitidae (Amphoridea; if belonging to the Carpoidea *Eocystites* BILLINGS, emend. BATHER, should be excepted, cf. BATHER 1918, p. 55),<sup>19</sup> Cryptocrinitidae, and Macrocystellidae (Aporita). To the genera included in these families may be added two more genera, erected recently, viz. *Bockia* HECKER 1938 (formerly interpreted by JAEKEL 1900, p. 627, as "sackförmige Anhangsorgane" and 1918, p. 124, as "sackförmige Wurzelblasen" of *Rhipidocystis*!) and *Lepidocystis* FOERSTE 1938.

The Eocrinoidea range from the Lower Cambrian to the Middle Ordovician.

### Class Paracrinoidea nov.

The forms, for the reception of which the new class Paracrinoidea is proposed, have for a long time been the subject of very different opinions

<sup>18</sup> In this group were also included the Comarocystitidae and the Malocystitidae, which are in this paper tentatively referred to a new class, the Paracrinoidea.

<sup>19</sup> ZITTEL-BROILI (1924, p. 219) referred the Eocystitidae to fam. Aristocystitidae (Diploporita).



with regard to their systematic position. The genera concerned are *Comarocystites* BILLINGS, from the Middle Ordovician (Trenton) of Canada and Ohio (FOERSTE 1920 b, p. 38), and its allies. *Comarocystites* was erected in 1854 and further mentioned by BILLINGS 1857 (p. 288) and 1858 a (pp. 61—63). HAECKEL (1896, p. 64) placed it in the exceedingly heterogeneous family Palaeocystida of his order Amphoridea. BATHER 1900 (p. 55) and 1913 (p. 426, § 262) referred it to the Rhombifera, JAEKEL 1900 (p. 676) to the suborder Brachiata of his Carpoidea Eustelea, SPRINGER 1913 (p. 151) to the Amphoridea, and so did BASSLER 1938 (p. 9). JAEKEL 1918 (p. 27) was doubtful about the proper treatment of *Comarocystites* and appended it — along with *Amygdalocystites* BILLINGS — to the Eocrinoidea with the following reservation: — “Wenn sich diese bisher nicht nachgeprüfte Angabe [uniseriality of exothecal subvective appendages, BILLINGS] bestätigt, müsste man mit der Möglichkeit rechnen, dass C. auch ein entgleister höherer Crinoidentypus sein könnte, da derartig specialisierte Armbildungen innerhalb der Eocrinoidea bisher ganz unbekannt sind.” ZITTEL-BROILI 1924 (p. 223) took it (and the Eocrinoidea) as an appendix to the Hydrophoridea.

The revision of *Comarocystites* wanted by JAEKEL was already performed by FOERSTE and published in the paper ‘*Comarocystites* and *Caryocrinites*, cystids with pinnuliferous free arms’ (1916 a).<sup>20</sup> Regarding the systematic position of *Comarocystites*, FOERSTE gave no definite opinion but remarked (p. 110) that “the separation of these three genera [*Comarocystites*, *Amygdalocystites*, *Canadocystis* JAEKEL 1900] from the Rhombifera seems desirable”. BILLINGS’ observations of the structure of the subvective appendages were largely confirmed: “Evidently both the brachials and pinnulars of these two arms [present in a certain specimen; otherwise there are four of them] are arranged in uniserial order” (FOERSTE 1916 a, p. 88). In a later paper FOERSTE (1920 a, p. 196) again remarked that uniserial arms seem to be characteristic of a restricted, closely related group of forms, and that the structure cannot be considered primitive, since in all early genera (here referred to the Eocrinoidea) a biserial arrangement is present. Different opinions have been raised about the nature of these appendages. SPRINGER (1913, p. 151) spoke of them as “brachioles borne on processes”. ZITTEL-BROILI (1924, p. 222) interpreted them as “einzeilige Brachiolen — —, die zuweilen — — Seitenzweige besitzen”. Now, according to BATHER 1913 (p. 385, § 100), the “brachioles of Blastoids and Cystids differ from the Crinoid brachium, not merely in more fundamental features, but also in the fact that they are invariably biserial and present no trace of an anterior uniserial stage”. In consequence, the exothecal subvective appendages of *Comarocystites* should possibly be looked upon as homologous with the pin-

<sup>20</sup> For *Caryocrinites*, cf. above, p. 20, foot-note 6.

nulate brachia of crinoids. The arm structures of *Amygdalocystites* and *Canadocystis* were thought by FOERSTE (1916 a, p. 71) to be much the same as in *Comarocystites*, though the arms are not free but recumbent.<sup>21</sup> This indicates clearly, that *Comarocystites* and allies are "not normal cystids" (FOERSTE 1916 a, p. 71), but join in this respect the Crinoidea. On the other hand there are features that prevent us from ranging the forms under consideration as crinoids.

Thus e.g. it proved impossible to demonstrate in *Comarocystites* "the presence of any radial plan of arrangement of the lower thecal plates, extending outward from a supposed primary basal series" (FOERSTE 1916 a, p. 79). There is no differentiation into calyx and tegmen. Further *Comarocystites* possesses a pore-system, which does not, however, penetrate the whole of the thecal wall but is confined to the stereothek, being covered by an epithek, recalling the conditions in *Echinospaerites*. Also in *Amygdalocystites* pores are present, which are not visible in unweathered specimens in external view. In *Canadocystis* no pores have been stated.

Summarizing what has been said above, we arrive at the following diagnosis of *Paracrinoidea* nova classis: —

A class of *Pelmatozoa*, the plate-system of which is not affected by polymeric symmetry and shows no differentiation into a calycinal and a tegminal portion; the exothecal subvective skeletal appendages are developed as uniserial brachia (free or recumbent) bearing uniserial pinnulae; a sub-epithecal pore-system is present in typical forms.

To this class belong *Comarocystites*, *Amygdalocystites* (cf. yet footnote 21 below), and *Canadocystis*, the last mentioned of which has no pores but seems to agree closely with *Amygdalocystites* in other respects. Of other genera referred by BASSLER 1938 (p. 9) to the families *Malocystitidae* and *Comarocystitidae*, *Malocystites* BILLINGS is insufficiently known. FOERSTE (1920 b, p. 38) remarked that it is so unlike *Amygdalocystites* and *Canadocystis* with regard to the development of the plates supporting the subvective appendages "that close relationship remains in doubt". *Platycystites* S. A. MILLER was, according to BATHER (1900, p. 51), "based on a worn *Anomalocystid* of indeterminable affinities". From the description of *Wellerocystis* FOERSTE (1920 b, p. 36 seq.) the structure of the supposed pinnulae is not clear; nothing was said of the presence of a pore-system. The genus was stated, however, to be closely related to *Amygdalocystites* and, especially,

<sup>21</sup> It should be observed that RAYMOND (1921, p. 3) proposed the free thecal appendages in *Amygdalocystites* to be made up of biserially arranged plates, "those of the two sides being opposite in position instead of alternating as in *Pleurocystites*". If this is true, *Amygdalocystites* would rather be interpreted as belonging to the *Rhombifera*.

*Canadocystis*. The unique specimen of *Achradocystites* well described by VOLBORTH 1870 (p. 9 seq.) is too imperfect for a determination of its affinities. It was placed with the Comarocystitidae on account of a certain structural resemblance of its plates to those of *Comarocystites* (BATHER 1900, p. 56).

All Paracrinoidea are Middle Ordovician of age.

### Class Carpoidea.

An extremely important section of JAEKEL's 'Phylogenie und System der Pelmatozoen' is that dealing with the Carpoidea (1918, p. 113 seq.). It is true that this class had been established by JAEKEL several years before, but his communication of 1900 had, in several respects, a rather provisional character. The term Carpoidea was, indeed, used by the same author as a nomen nudum already in 1899 (pp. 63, 159, &c.) and their independent position in relation to the cystoids was strongly emphasized (p. 160).

While the new class was accepted e.g. by SCHUCHERT (1904, p. 204), it was at first met with a severe — and, as it must be confessed, useful — criticism by BATHER (1913, p. 364 seq., § 16), which, however, overshot the mark, as the subsequent evolution of the opinions about the carpoids showed.

Part of the "Cystidea(?)" characterized by BELL (1891, pp. 209, 212) as "Caliculata Anactinogonidiata" (i.e. forms with bilaterally symmetrical or asymmetrical gonad) correspond to the Carpoidea.

A great merit of JAEKEL's investigation is to have settled the account with the exceedingly heterogeneous class Amphoridea, founded by HAECKEL in 1895 and unfolded further in his unfortunately too fanciful work of 1896 (p. 9 seq.). JAEKEL showed, how the class Amphoridea had to be dismembered into very different groups of Hydrophoridea and Carpoidea (and, as we may add, Paracrinoidea and Eocrinoidea). The value of this statement was in part obscured by BATHER's ranking JAEKEL's carpoid order Heterostelea as a suborder of Amphoridea, the latter conception yet being used in a revised sense. But, on the other hand, he advocated the view, after that generally held, that the Eustelea of JAEKEL have no domiciliary rights in the Carpoidea (BATHER 1913, p. 365, § 19). This was accepted in deeds and words also by JAEKEL (1918, pp. 118—119). Thus the group Carpoidea corresponds only to the Heterostelea of JAEKEL 1900. Still in 1926 BATHER (in WITHERS 1926, p. IX) spoke, however, of "the ill-defined assemblage of Cystidea called Carpoidea by JAEKEL, or the no better defined Amphoridea HAECKEL em. BATHER". Only a few years later, in his article on Echinoderma in 'The Encyclopedia Britannica', BATHER (1929 a, p. 898) stated that the "Carpoidea are now distinguished as a class". And in two papers with mutually similar



contents (BATHER 1929 b; 1930) he discussed the organization of carpoids and arrived at the conclusion that, along with the Machaeridia of WITHERS, they "constitute a totally distinct Branch, which may be named *Echinoderma bilateralia* as opposed to *Echinoderma radiata* (1930, p. 435). All the more it is to be regretted that BASSLER 1938 did not take notice of BATHER's readjustment of position but recorded HAECKEL's Amphoridea as an order of the class Cystoidea. — ZITTEL-BROILI (1924, p. 12; also in preceding editions of the text-book) took the Carpoidea as an order of Cystoidea. Considering i.a. the lack of thecal pores, distinguishing them from the Cystoidea, and the usually bilateral symmetry of the theca, so unfamiliar to most echinoderms as pointed out by BATHER, as well as the biseriality of the stem, it must be considered to be well-advised to look upon the Carpoidea as a distinct class.

Some recent investigators have, on the other hand, thought it evident that the limits of Carpoidea towards other groups are not sharply defined, a statement which does not, however, affect the validity of ranking them as a separate class. For more or less pronounced intermediate or transitory types are to be found between all categories of taxonomic units, as is well known to every paleontologist.

On the evidence supplied by the American genera *Iowacystis* THOMAS & LADD 1926 (cf. the systematic part) and *Amecystis* ULRICH & KIRK 1921 — the latter genus being nearly coincident with *Pleurocystites* but for the rhomb-pores, which are entirely absent — DEHM (1934, p. 36 seq.) proposed a closer affinity between certain Carpoidea and certain Hydrophoridea. The Pleurocystitidae (including the Lower Devonian *Regulaecystis* DEHM 1933; Germany) were said to be more closely related to the Carpoidea Soluta than to the Hydrophoridea Rhombifera. This opinion cannot be accepted, however. DEHM even proposed to divide the Cystoidea, excluding the Edriasteroidea ("Thecoidea", Hydrophoridea, and Carpoidea were taken as orders of the class Cystoidea; cf. DEHM 1933, p. 64), into three groups: 1. Cincta-Mitrata-Cornuta. 2. Soluta-Pleurocystitidae. 3. Hydrophoridea. Group 2 was considered a passage group between 1 and 3 (DEHM 1934, p. 40).

Also HECKER 1940 (pp. 63—64), in connexion with his revised description of *Rhipidocystis* JAEKEL, pointed out the relationship between the Carpoidea and the Hydrophoridea. But he would not confirm the arrangement of DEHM just quoted. HECKER discussed the classification of the Carpoidea and added to the orders established by JAEKEL 1918 the new order Digitata HECKER 1938 to include *Rhipidocystis*, which differs from other known carpoids by having strongly developed brachioles. He further emphasized that our knowledge of these, as a rule, rare fossils is still very imperfect, which should urge to caution at the interpretation and classification of the carpoids (HECKER 1940, p. 64). As for *Rhipidocystis* one could express the

opinion that, in certain respects, it does not fit well into the general model of Carpoidea.

In a stimulating article on evolution in Echinodermata, W. K. SPENCER (1938, pp. 301—302)<sup>22</sup> suggested "that the present subdivision of the Echinodermata into Pelmatozoa and Eleutherozoa be replaced by a new subdivision, the Dactylozoa and the Podozoa", the last-mentioned having tentacles, the first-mentioned having no tube feet but collecting their food by ciliary currents created on brachioles. As for the Carpoidea the classification proposed would mean, according to SPENCER, that the "Carpoidea sensu stricto" be referred to the Podozoa along with the Crinoidea, the Asterozoa, the Echinoidea, and the Holothurioidea, whereas the Carpoidea Soluta ("*Dendrocystis* and its allies"), the Hydrophoridea, the Blastoidea, and the Edrioasteroidea be referred to the Dactylozoa. — It may be remarked that a classification based on physiological facts was advanced several years earlier by W. J. SOLLAS (1899, p. 715), who proposed to arrange the Echinodermata into two sections: Microphagi (corresponding to the Pelmatozoa) and Megophagi. The first-mentioned "obtain their food as it were in molecules, by ciliary action; the other Echinodermata ingest it in larger masses by a prehensile mouth or jaws".

Attempts to advance a classification based on the mode of feeding are not tenable, as appears from investigations concerning the ciliary currents on the body-surface in echinoderms which were carried out by GISLÉN (1924). Here it was demonstrated i.a. how in certain asterids detritus is brought to the mouth by ciliary currents (p. 266).

SPENCER's theses were denied in a paper by GENEVIÈVE DELPEY (1942 a) which the present author unfortunately knows only from the abstract by W. E. SCHMIDT.<sup>23</sup> Several of the arguments upon which SPENCER based his system proved to have no convincing force, and what concerns the carpoids several facts of importance for the matter have as yet not been explained definitively. Furthermore, it was suggested that the Carpoidea, the Rhombifera, and the Crinoidea be brought together by their having a stomodaeum, a hydropore instead of a madreporite, and a stem.

The carpoid organization seems to have been well adapted to environmental conditions, since the type survived from the Middle Cambrian until the Lower Devonian.

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<sup>22</sup> The functions ascribed by BATHER, JAEKEL, and GISLÉN to the two summit openings in the Trochocystidae were shifted by SPENCER, an interpretation that is in no way supported by actual features of organization.

<sup>23</sup> Zbl. Mineral. T. 4. Paläontologie. 18. — Berlin-Zehlendorf 1943. Abstr. 3048.

### Class Edrioasteroidea.

In the index of BASSLER (1938) and in the text-books of ZITTEL-BROILI (1924), and SPRINGER (1913), to take some examples, the Edrioasteroidea were ranked as an order of the class Cystoidea. But usually these groups have been disposed side by side, after JAEKEL having in 1895 (p. 110) defined the "Thecoidea" as a separate division of the Pelmatozoa. Thus the Edrioasteroidea were looked upon as a class e.g. by JAEKEL (1899 and 1918, under the name of Thecoidea); BATHER (1899, 1900, 1929 a); MACBRIDE (1906); BASSLER (1935, 1936). ABEL (1920) made the Crinoidea, the Cystoidea, the Carpoidea, and the "Thecoidea" subclasses of the class Pelmatozoa. HAECKEL (1896), whose interpretation of morphology and taxonomy of the fossil non-crinoid Pelmatozoa turned out to be in essential respects very unsuccessful, classified the "Agelacystida" as a family of his class Cystoidea.

A partially new classification of the Echinodermata was outlined by MATSUMOTO (1929). They were divided into three subphyla: — Crinozoa (tolerably corresponding to the Pelmatozoa), Echinozoa, and Asterozoa. Of interest to us in this connexion is that the Edrioasteroidea were listed as a class of subphylum Asterozoa. The reason for this was no doubt that the Edrioasteroidea are accepted by most authors as the ancestral group from which the Eleutherozoa were derived. This may be true but has no influence upon the fact that the Edrioasteroidea are organized throughout according to the pelmatozoan type (oral surface directed upwards, presence of a subvective system of ciliated grooves, &c.), on account of which they have to be referred in formal respect to the Pelmatozoa. Moreover, it has been also proposed that the Edrioasteroidea became extinct without having given rise to any descendants, but conclusive arguments have not been set forth (MACBRIDE 1906, p. 596; ABEL 1920, p. 282). To these authors it seemed improbable that freemoving organisms, with the ventral surface directed downwards, could rise from the statozoic edrioasteroids, the ventral surface of which is consequently directed upwards. Contrary to this opinion instead we have to assume that the Eleutherozoa were derived from primitive forms with the ambulacral surface directed upwards (cf. GISLÉN 1934, p. 4).

It is obvious that the Edrioasteroidea have several points in common with forms referred to other classes of Pelmatozoa. But on the other hand there are characters — such as the lack of exothecal subvective appendages, and the presence of pores (for podia) between the ambulacral elements or between those and the thecal plates — which fully justify the ranking of the Edrioasteroidea as a separate class. In stating this it should of course not be concealed that in many respects the interrelations between the Edrioasteroidea and the Cystoidea are still obscure. The account (by W. K. SPENCER) of "various forms (including the Edrioasteroidea) allied to the cystids",



of which MACBRIDE & SPENCER (1938, p. 134) held the prospect, is therefore looked for with special interest (at least so far as the present writer knows, it has not been published yet).

The Edrioasteroidea include a number of rather heterogeneous forms, referred to different families. No attempt has been made, however, to group the families into orders. — Range: — Lower Cambrian—Lower Carboniferous.

### Incertae sedis:

#### Cyclocystoidea MILLER & GURLEY 1895.

Ever since their first appearance in paleontologic literature, the rare forms referred here have puzzled the investigators which have had occasion to a closer study of these peculiar organisms. This is due to the fact that their organization — as far as it has been possible to make out from the fossil material hitherto available — is in several important points still obscure and seems to differ in essential respects from that of other known classes of echinoderms. Unfortunately the Swedish specimens of *Cyclocystoides* studied by the present writer have not contributed to bring the question of classification nearer to its solution.

Most authors dealing with the matter have consented in placing *Cyclocystoides* with the Pelmatozoa. It is true, however, that with regard to mode of life the forms in question seem to have been more or less eleutherozoic, since a point of attachment has not been observed in any specimen. Further, we have not obtained a clear view of the location of mouth and anus. On the whole it must be admitted that, in general appearance, *Cyclocystoides* does not seem to come very close to other known Pelmatozoa. According to the interpretation advanced by BEGG (1934, p. 223), the plate containing all organs essential in the economy of the animal was the lower one, being covered by another plate called dorsal. We have to imagine that a system of radial ducts was developed between the lower plate and the upper one bringing water from the submarginal canal surrounding the central disk (cf. the description of the Swedish forms given below (to a supposed central mouth. The diameter of the dorsal plate was, of course, smaller than that of the ventral plate so as not to cover the circular submarginal canal. This canal, then, has to be looked upon as a sort of ambulacral groove forming part of an ambulacral system, the development of which is throughout unique. Excepting the circular canal, this system is entirely hypothetical. As emphasized RAYMOND (1913, pp. 30–31), “no echinoderm is known in which the food groove is not radial, instead of circular, and does not lead directly to the mouth”. HERTHA SIEVERTS[-DORECK] (1934, p. 975), in her

review of BEGG's paper on *Cyclocystoides*, asserted that the radial rays of the lower plate would be corresponded by ambulacral grooves of the upper face. This does not seem to be corroborated by actual conditions. On the contrary, FOERSTE (1924, p. 81) stated conclusively that "no system of arms [i.e. ambulacra] was incorporated in the disk as in *Agelacrinus*, and related genera" (it should be noted that by analogy from the orientation in "normal" pelmatozoans, the upper plate was called "ventral" by FOERSTE, and the lower plate "dorsal"). SIEVERTS further proposed that the spoon-shaped depressions of the outer portions of the submarginal area present in BEGG's specimens be brachiole facets. This seems to need confirmation by additional observations, especially with regard to the fact that in specimens which are not casts or impressions — as are the specimens described by BEGG — the so-called spoon-shaped depressions present themselves as elevations.

In spite of the very aberrant organization of *Cyclocystoides* outlined here, it might be justified to refer the genus (and its allies *Narrawayella* FOERSTE 1920<sup>24</sup> and *Savagella* FOERSTE 1920) to the Pelmatozoa, especially on account of the proposed presence of a subvective system of ducts. As mentioned, this is also the view of most authors who have expressed an opinion about its systematic belonging. In this respect HALL 1872 (p. 219) formed an exception, for he found *Cyclocystoides* to "resemble the Echinidae of succeeding geological periods more than the Crinoidea, Cystidae or Asteridae of the Palaeozoic formation".

If the interpretation of the organization here indicated is correct, *Cyclocystoides* would be another instance of achieving protection for the ambulacral system, an aim that was realized in different ways in other pelmatozoans (cf. GISLÉN 1934, p. 14 seq.).

Accepting the pelmatozoic nature of *Cyclocystoides*, we have to consider its position in relation to known pelmatozoans. SALTER & BILLINGS, who erected the genus, were inclined to take it for a cystoid with regard to "a not indistinct resemblance to such forms of Cystideae as *Pseudocrinites* — —, or perhaps still nearer to the Canadian form *Amygdalocystites*" [Paracrinoidae] (1858, p. 90). The proposed resemblance is merely superficial, however. Also Asteroidea were implicated in the discussion by the authors quoted. Subsequent American writers (MILLER & DYER 1878; MILLER 1881; FABER 1886; MILLER & FABER 1892; MILLER & GURLEY 1895), who described several species of *Cyclocystoides*,<sup>25</sup> partly insufficiently defined, did not contribute to throw light upon the matter of classification. In 1900 BATHER

<sup>24</sup> To the present writer this genus seems to be weakly defined.

<sup>25</sup> *Cyclocystoides cincinnatiensis* MILLER & FABER 1892 was made the genotype of *Narrawayella* FOERSTE 1920.

(p. 210) suggested that it might probably belong to the Edrioasteroidea, though not to any of the recognized families. This view was shared by SPRINGER (1913, p. 159), FOERSTE (1920 b, p. 35), ZITTEL-BROILI (1924, p. 211), and BASSLER (1935, p. 10; 1938, p. 13). RAYMOND (1913, pp. 30—31) presented two alternative interpretations: either *Cyclocystoides* "was a free Cystidean or Edrioasteroid" or "the highly specialized root of a free crinoid" to be compared with the plated, discoid bodies of *Lichenocrinus* with their lamellous radiate structure. In view of the very differentiated construction of *Cyclocystoides* the second alternative does not seem to be very likely. Further there is nothing to indicate a point representing the cicatrix of a stem.

The last time *Cyclocystoides* was discussed at some length, was by BEGG 1934, who made a careful investigation of a few specimens from the Ashgillian of the Girvan District. From the study of this material BEGG (1934, p. 224) concluded "that *Cyclocystoides* has its affinities with the Cystidea and may even represent a distinct order of that class".<sup>26</sup> In the passage just quoted, the word "Cystidea" should most likely be changed for "Carpoida", in accordance with the comprehension of these conceptions recommended in the present paper. For BEGG seems to have advocated his view of the relations of *Cyclocystoides* in the first hand on account of a proposed analogy in mode of life between that organism and *Cothurnocystis*. The mentioned author was "struck by the resemblance of the spoon-shaped depressions to the grooves with their cover-plates in the subvective system of Bather's two species, particularly in the case of *C. elizae*" (BEGG 1934, p. 223).<sup>27</sup> Here we must again call attention to the fact that the "spoon-shaped depressions" are no primary structures. In the opinion of the present writer the affinity to the carpoids might not be very close.

FOERSTE 1924, in redescribing *Cyclocystoides huronensis* BILLINGS, gave no opinion of its affinities. JAEKEL (1899; 1918) did not even mention the genus.

<sup>26</sup> For the reception of *Cyclocystoides*, MILLER & GURLEY 1895 (p. 61) established the order Cyclocystoidea, as we have seen above.

<sup>27</sup> Authors dealing with the subject do not agree with BATHER (1913, § 230 seq.; 1926, p. 6 seq.) in interpreting the slit-like openings in the obverse side of the theca of *Cothurnocystis* as having had subvective functions. JAEKEL (1918, p. 115) suggested that the pores were outlets for sexual products. GISLÉN (1930, p. 206) found this extremely improbable, because it would imply an internal segmentation of the theca. Furthermore, he thought the series of pores to be a drainage organ for excess water from the anal intestine for preventing too much dilution of the nutritive pulp (GISLÉN 1930, p. 212). SPENCER (1938, p. 299), finally, proposed the slits to have been "respiratory pouches probably without any communication with the alimentary canal". The aperture generally looked upon as an anus according to SPENCER, is "the mouth of a vestibule which held mouth and anus".



That *Cyclocystoides* was placed with the Edrioasteroidea by BATHER and others is due, of course, to its discoid shape and its more or less squamose plating. As informed us MAILLIEUX (1926, p. 94) in a communication of a remarkable find of *Cyclocystoides* in the Lower Devonian of Belgium, BATHER himself thought "que l'attribution de *Cyclocystoides* aux Edrioasteroïdes ne pourra pas être maintenue". BASSLER (1936, p. 23) stated that the fam. Cyclocystoididae "must be left at present as an uncertain order of Pelmatozoa" (yet, as mentioned, BASSLER 1938 appended it to his order Edrioasteroidea).

The present writer cannot but agree with the spirit of this declaration. The scanty fossil material available does not, however, admit of any safe conclusions. But it would not be surprising if the Cyclocystoidea will prove to be referred conveniently to a separate class. So we have only to abide that, some day, positive data of the organization of *Cyclocystoides* will be secured on evidence of specimens more favourable for observations so as to shed light on its real position and interrelations to other echinoderms.

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[Machaeridia WITHERS 1926.

A few words will be said of the so-called Machaeridia, which are here put within brackets, for — in accordance with WOLBURG (1938) — the present writer cannot find that they are echinoderms at all. After the publication in 1926 of WITHERS' paper on *Turrilepas* and its allies, they were, however, accepted almost generally as echinoderms. This, moreover, is only natural if we consider that the hypothesis was supported by BATHER, the great authority on the subject.

It is equally intelligible that the machaerids had by most earlier authors been interpreted as cirripeds, as first proposed by H. WOODWARD (1865), until this was called in question by WITHERS. In his revision of the group WITHERS pointed out several structural features supposed to indicate the echinoderm nature of these fossils but did not vindicate his opinion categorically ("Whether they be accepted as Echinoderms or not", &c., WITHERS 1926, p. 84). He considered, however, that the machaerids might in the first place be shown to belong to the Cystoidea, "having in mind the widely divergent forms included — — in that group or even some new group of Echinoderms just as anomalous as are the Cystids" (WITHERS 1926, p. 83). BATHER, in the preface to WITHERS' paper (1926, p. XI), came to the tentative conclusion "that the Heterostelea [=Carpoidea] and Machaeridia are among the earliest offshoots from the Echinoderm stem of which we have knowledge; that, though in several respects the Machaeridia resemble certain Heterostelea, yet they are not Heterostelea, and are not descended from

Heterostelea; that these two Classes, for so on this hypothesis one must regard them, differ from all other Classes of Echinoderma in not having had pentamerism and the other echinoderm features impressed on them during an ancestral period of fixation". That he was still in doubt how to fix definitely their position is evident, however, from the way in which he referred to them in subsequent writings. Thus two years later he stated that the Machaeridia, along with a few other groups, "differ so greatly from any creatures now known to us that we are uncertain where to place them" (BATHER 1928 b, p. XCVI). In his classification of the Pelmatozoa communicated in 'The Encyclopedia Britannica' (BATHER 1929 a, p. 898) he recognized two main sections, one of which, "with no trace of radial structure", comprises Machaeridia and Carpoidea. Later (BATHER 1930, p. 435) the two classes were said to "constitute a totally distinct Branch, which may be named Echinoderma bilateralia as opposed to Echinoderma radiata".

From the researches here briefly related, it seems to have appeared — irrespective of the correctness of the rest of the suggestions — that the Machaeridia have to be removed from the cirripeds. This was confirmed e.g. by CHERNISHEV (1935, p. 35), who pointed out that the primitive ancestors of the true Cirripedia, which do not appear until in the Trias, are completely unknown, whereas the position of the Machaeridia be doubtful.

WITHERS' suggestions were met with a severe criticism by WOLBURG (1938), who denied the argument, article by article. After a study of Swedish material — that described by MOBERG 1914 a and b (LM), and collections from the Silurian of Gotland (RM) — the present author has to agree in refusing the echinoderm theory for the machaerids. The crystalline cleavage thought to be significant of echinoderms could not be stated to occur in typical appearance in any specimen as far as the writer is aware. In fact WITHERS (1926, p. 84) observed that "the fossilisation of the plate as a single crystal of calcite is seen only in certain species of *Lepidocoleus*". And, further, as emphasized by WOLBURG (1938, p. 296): — "The clear existence of the cleavage plates in *Lepidocoleus* shows that if they are not Echinoderms, then this condition of fossilisation is not restricted to Echinoderms stereom".

The main objection of WOLBURG — quite noteworthy in the opinion of the present author — may be quoted in extenso: — "Das Skelett der Machaeridia widerspricht in seiner Anlage dem Sinn eines Mesodermalskelettes vollkommen und zeigt nicht die den Echinodermen eigene orientierte örtliche Durchbrechung einer Kapsel durch verschiedene Organe, sondern vielmehr einen Apparat, der in seiner ganzen Länge an zwei getrennten Rändern dem Öffnen und Schliessen zum Zwecke der Respiration oder Ernährung angepasst ist und nicht in einem ringsumliegenden Mesenchym entstanden sein konnte" (WOLBURG 1938, p. 297).

There is no need in this connexion further to dwell upon the problem of Machaeridia. It may only be mentioned that WOLBURG was inclined to refer them to the Mollusca, possibly an unknown group uniting in itself features from the Placophora (the first machaerid made known to science, in 1857 by DE KONINCK, was described as *Chiton*!) and the Lamelli-branchiata.

The Machaeridia were not considered in the classification of Echinodermata outlined by MATSUMOTO (1929). On the other hand the class Ophiocistia SOLLAS 1899, emend. HECKER 1938, was appended to MATSUMOTO's subphylum Crinozoa, which corresponds to the Pelmatozoa, only that the Edrioasteroidea were referred to the Asterozoa. MATSUMOTO (1929, p. 31) remarked about the Ophiocistia that the "arm-rami, which appear to have been a locomotive organ, might possibly have been derived, though very distantly, from Cystid brachioles of a certain type". From the researches of FEDOTOV (1926) into these peculiar organisms it is evident, however, that the so-called arms of Ophiocistia are homologous with the ambulacral podia of Ophiuroidea and other Eleutherozoa, as previously suggested by BATHER. Also, with regard to certain features of the disk, homologies with the Ophiuroidea can be traced (FEDOTOV 1926, p. 1152). So there can be no doubt of the eleutherozoic nature of the Ophiocistia, as stated by most authors. Only as to the taxonomic rank of the group the opinions have differed a little. In 1912 SOLLAS & SOLLAS (p. 222) defined the Ophiocistia as a separate class of Eleutherozoa. This was also the viewpoint of e.g. FEDOTOV (1926), RICHTER (1930), and HECKER (1938 b; 1940 b). BATHER (1929 a, p. 898) took them for "modified Stelliformia or Echinoidea" that "cannot be maintained as a separate class". ZITTEL-BROILI (1924, p. 240) mentioned the Ophiocistia among the Ophiuroidea but remarked that their position was doubtful. SCHUCHERT (1915, p. 275 seq.) listed them among "Forms whose relationships are unknown" as an anomalous order of Eleutherozoa. The question of the strict systematic status of Ophiocistia needs no consideration in this connexion, but it may be mentioned that the Ordovician genus *Volchovia* HECKER 1938 — the earliest representative of the group — presents a feature recalling the Hydrophoridea, viz. an anus covered by a pyramid of valvules, whereas in the younger forms the anus seems to be lacking (HECKER 1938 b, p. 427; 1940 b, p. 75). And the Silurian *Eucladia* WOODWARD 1869 was said by FEDOTOV (1926, p. 1154) to have "general resemblance to the Cystidea" with regard to the position of madreporite and genital pores near the mouth, which was supposed to corroborate the theory of the origin of Eleutherozoa from Pelmatozoa. Lately MACBRIDE & SPENCER (1938, p. 95) stated the Ophiocistia to have certain characters in



common with the Upper Ordovician *Eothuria* MACBRIDE & SPENCER 1938, referred to the Holothuria but said to approach the Echinoidea in several respects.]

In the above discussion of the classification of the Pelmatozoa, being based on fossil material, we have had, for natural reasons, to pay attention almost exclusively to characters connected with the structure and arrangement of elements belonging to the skeleton system. It is obvious, however, that the development of the external skeleton displays important features of the internal organization on account of a certain correlation.

## Selected Points of the Morphology of Cystoidea.

The general morphology of the cystoids has been investigated and elucidated so exhaustively, first and foremost in the great memoir of JAEKEL 1899, that in most respects not very much has to be added. What will be said here in a few words about certain points of the matter and of the use of certain terms, refers in applicable parts also to other non-crinoid Pelmatozoa than cystoids. It is true that important features of organization are still obscure, maybe in the first hand in the case of the Carpoidea. There is no reason, however, in this connexion to deal with the group mentioned, since it is almost unrepresented in Swedish series of strata.

The mesodermal skeleton in the Cystoidea forms a capsule, being the general envelope of the intestine. For this capsule the term *theca* is used here. The reason why "theca" should be preferred to "calyx" (German "Kelch") was presented by HECKEL (1896, p. 13), who pointed out that the capsule of the Cystoidea is not — or not as a rule — differentiated in a way similar to that of the corona of the Crinoidea, which (exclusive of the arms) consists of the dorsal calyx (patina) and the ventral tegmen. JAEKEL (1899, p. 74) sharpened the conception "theca" so as to refer only to the very primary wall of the body. Even in recent literature the term "calyx" is used sometimes synonymously with "theca", however.

The pores penetrating the skeleton plates have been emphasized repeatedly above as an essential feature of cystoid organization. MÜLLER (1853, pp. 184, 186) distinguished two types of pores: "Porenrauten" (pore-rhombs, for a specialized form of which FORBES 1848, p. 485, introduced the term "pectinated rhombs", now usually written "pectinirhombs") and "Doppelporen" (diplopores). The first-mentioned are composed structures of canals arranged perpendicularly to and bisected by the sutures of plates and developed in different ways. The diplopores, which do not, like the pore-rhombs, have their long axis parallel with the surface of the plates but perpendicular to it, are usually distributed irregularly over the plates and do in most cases not extend over the suture between two adjacent plates.

So the whole system of a diplopore lies regularly within one and the same plate.

BATHER (1928 b, p. LXXXII) remarked that the pore-rhombs of Rhombifera may resemble diplopores, as in *Echinosphaerites*, where the folds are roofed over, except at their two ends. An appearance very similar to that of a diplopore may further arise from a shortening of the long axis of a pore-fold, as observed the present writer in a young specimen (diam. about 7 mm) of *Heliocrinites granatum* (WAHLENBERG) [RM Ec 4468], shown in Pl. 1, fig. 1. It would not be justified, however, to conclude from this that the pore-rhombs were derived from diplopores. JAEKEL (1899, p. 116 seq.) discussed the relation of the different pore types to one another, and arrived at the conclusion that the diplopores are a structure secondary to the pore-rhombs, which also may be confirmed by the fact that the Rhombifera appeared, as far as known, earlier than the Diploporita.

JAEKEL (1899, p. 120) emphasized that the different types of pores must have been physiologically equivalent. Nor can it be doubted nowadays that they performed a respiratory function, being — besides the ambulacral and alimentary systems — the only organs by which aërated water could come into contact with the body-fluids for oxygenation by osmosis. And it is likely that the main respiration process took place by the pores. For natural reasons it is namely probable that the alimentary system served in the first hand feeding and excretion purposes, whereas the ambulacral system seems to have been essentially a hydraulic mechanism for regulation of the interior pressure (BATHER 1928 b, p. LXXXI). In the case of pore-rhombs and hydrospires, the water passed into their folds. A similar circulation may have taken place in the U-shaped canals of the diplopores, or a papula (papilla) projected from each diplopore (cf. BATHER l.c.).

In view of the function of the pores, it is only natural that in such forms as were attached to the substratum directly without intermediation of a stem, the very base-surface is devoid of pores. This, moreover, was stated expressly by LOVÉN (1867, p. 438) for *Sphaeronites*. It may be mentioned, however, that in a few instances the present writer found pores to be developed also on the surface of attachment of *Sphaeronites* (Pl. 1, figs. 2—3). But there is no reason to interpret this accidental occurrence of pores otherwise than as an anomaly.

It is obvious that in times past it would happen that the diplopores were mistaken for exits of ambulacral feet, for there is, indeed, a very great morphologic resemblance between them and the paired openings for the podia in Echinoidea. This certainly seemed to GYLLENHAAL (1772) to support his theory of the belonging of the Hydrophoridae to the Echinoidea. As we have seen above (p. 16), his opinion was shared by other older authors too. MÜLLER already (1853, p. 183) pointed out, however, that on account of



their interambulacral position as well, the diplopores cannot possibly be ambulacral pores: "Ihre Bedeutung ist unbekannt, gewiss ist nur, dass es nicht Durchgänge von Saugern sind. Es liegt der Vergleich mit den respiratorischen Poren der Asterien nahe . . .". Therefore it is surprising that LOVÉN adopted GYLLENHAAL's proposition about the nature of the diplopores. A quotation will prove this: "It was, no doubt, a bright thought of J. A. GYLLENHAAL, in those days, now more than a hundred years ago, to assimilate the 'cancelli' of the 'crystal apples' to those of recent Echini, and on that account to transfer their bearers to the animal kingdom, ranging them under the great natural genus *Echinus*, then recently instituted by LINNAEUS. And so close is in reality, on either side, the general conformity in structure of the geminous pores, as to cause the lineage of the Archaeonomous Echinoidea to gravitate forcibly towards that group of antique Cystoidea of the Silurian era, different as these no doubt were in other respects, in the total absence, — at least in the adult, — of a calyx, and in the distribution of the pores all over the perisome. There seems also to be little reason for doubting the pedicellar character of the geminous pores in *Sphaeronis*, *Eucystis*, *Glyptosphaera*, *Protocrinus*, *Mesites*, the less so since the want of a decisive proof in this regard is supplied, in some degree at least, by the occasional preservation of the actual pedicels in a contemporary form of Echinoids, *Bothriocidaris Pahleni* FRED. SCHMIDT, of the older Silurian era." (LOVÉN 1883, pp. 56—57.)

As pointed out by BATHER (cf. MORTENSEN 1928, p. 106, foot-note 1), the "resemblance of the diplopore to a podial pore, already noted by LOVÉN, is due to the fact that both papula and podium [for which LOVÉN used the term pedicel] subserve aëration by an up-and-down current of the contained fluid". In the same note communicated by MORTENSEN, BATHER proposed that the structures observed in *Bothriocidaris*, which are, moreover, restricted to the ambulacra, may equally be interpreted as ordinary diplopores, the external marking being the trace of the papula rising from each diplopore. We cannot give a definite answer to the question whether the organs proceeding from the pores are homologous with the tubefeet of true Echinoidea, or whether they are papulae (papillae) of diplopores (cf. MORTENSEN 1935, pp. 8—9). It need not be mentioned further that the conditions in *Bothriocidaris* do not in any case corroborate the opinion of the diplopores of Diploporita as openings for ambulacral podia.<sup>1</sup>

<sup>1</sup> The remarkable genus *Bothriocidaris* EICHWALD 1860, from the Middle and Upper Ordovician of Estonia, has given rise to a rather extensive literature, which there is no reason, however, to review in detail in this connexion. Generally *Bothriocidaris* has been considered an ancestor of Echinoidea. BATHER (1931, p. 60) took it for "an Echinoid which left no descendants". After the investigations of MORTENSEN (1928, 1930), *Bothriocidaris* may be looked upon rather safely as "the last, most specialized offshoot from the

In consequence of his opinion about the nature of the pores, LOVÉN (1883, p. 57) used the term "peripodium" for the structure of the Diploporita which is called in German "Porenhof". BATHER (1919, p. 113) proposed to reject the term "peripodium" — "along with the belief that it implies" — and substitute it by "peripore".

Most other authors, older as well as recent, have ascribed a respiratory function to the pore-system of the cystoids. In a paper, which is unfortunately known to the present writer only by the critical review by W. E. SCHMIDT,<sup>2</sup> G. DELPEY (1942 b), however, advocated the view that the pectinirrhombs are balancing organs. It seems to be wise — with W. E. SCHMIDT — to take up a sceptic position towards this theory, "zumal da der Wert eines solchen Organes nur für einen Teil der im Grundplan so gleichartig organisierten Pelmatozoen nicht ohne weiteres einleuchtet".

In discussing the pores of the Cystoidea, the present writer wants, finally, to point at the remarkable parallelism in mode of structure between the skeleton with its tube system of certain Hydrophoridae and the exoskeletal vascular system of the Cephalaspida, which was mentioned preliminary by W. K. SPENCER (1938, pp. 293—294), who held out the prospect of a more detailed investigation of the matter. In the light of the old theory of a connexion between the Echinodermata — especially the Carpoidea or a closely related branch of echinoderms, as suggested by MATSUMOTO (1929, p. 27) and further promoted by GISLÉN (1930, 1934) — and the vertebrate series, it would be of the utmost interest if it could be stated whether the startling similarity mentioned above is due to convergence, or whether it displays a deeper significance.<sup>3</sup> In this connexion it could be mentioned

Diploporite Cystids" (MORTENSEN 1930, p. 352). For historical reasons, *Bothriocidaris* was yet dealt with in MORTENSEN's magnificent 'Monograph of the Echinoidea' (1935), where his opinion of the phylogenetic significance of the genus was further explained and somewhat modified. The order Bothriocidaroida was placed as the unique order of subclass Pseudechinoidea MORTENSEN 1934. He admitted (p. 20) that "*Bothriocidaris* cannot properly be called a Cystid — — — but it can not more properly be called an Echinoid. It is something quite by itself". In 1938 MORTENSEN stated (p. 25) that the larval development of cidarids does not give "the slightest support of the *Bothriocidaris* theory" (taking *B.* as an ancestor of Echinoidea). — MORTENSEN's classification of the Bothriocidaroida was accepted e.g. by MACBRIDE & SPENCER (1938, p. 94) and KUHN (1939, p. 63).

<sup>2</sup> Zbl. Mineral. T. 4. Paläontologie. 18. — Berlin-Zehlendorf 1943. Abstr. 3049.

<sup>3</sup> In an interesting paper on 'Transformation of organic designs', GREGORY (1936) reviewed the origin of earlier vertebrates, arriving at assumptions very much agreeing with the theories advanced by GISLÉN (1930). By means of elimination he stated that no group but the Echinodermata can possibly lie in the line of ancestry to the vertebrates. "At first sight it would seem most fantastic to suggest that the sea lily could ever be transformed into the fish, and no doubt the typical crinoids are not in question. But while such a transformation is as yet far from being demonstrated, it must be admitted that one division of the Palaeozoic echinoderms, namely, certain families included under

that, according to JAEKEL (1918, p. 6), there is a certain similarity between the histologic development of the (mesodermal!) skeleton of Echinodermata and Vertebrata.

A great number of internal casts of *Echinosphaerites* (from Västergötland) show a system of grooved branching impressions, the course of which might appear from Pl. 1, fig. 4, and text-fig. 3. It is largely equal in different specimens. Our figures also agree fairly well with fig. 15 on Pl. 8 in JAEKEL 1899 showing the course of the proposed subthecal mesenteric septa in *Echinosphaerites*. The loop to the right of the mouth would represent the suboral septum enclosing the suboral sinus, and the vertical line the parietal septum according to JAEKEL. Much the same is visible in the specimen of *Deutocystites* (*Echinosphaerites*?) *modestus* figured by BARRANDE 1887, Pl. 16, fig. 5 (copied by JAEKEL 1899, Pl. 8, fig. 16). Corresponding structures have also been observed in *Echinoencrinites* and *Glyptosphaerites*, especially well developed in the last-mentioned genus (JAEKEL 1899, pp. 125—127). On comparison with the location of mesenteries in the larval *Antedon*, JAEKEL did not hesitate to infer that the impressions in question on the moulds indicate the peripheral course of septal structures in Hydrophoridae. A great importance is attached to the mode of development of the parietal septum as decisive of the extension of the rectum and the location

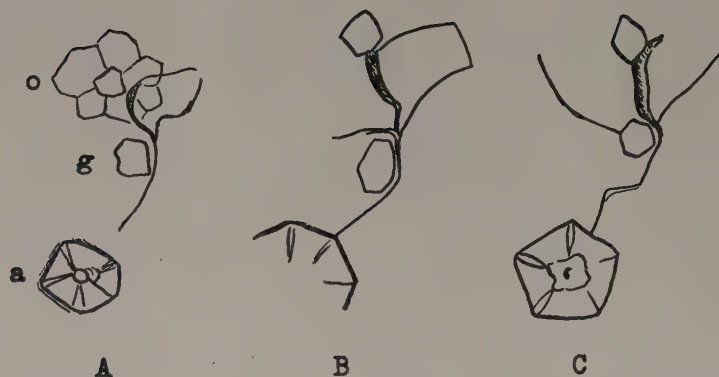
the subclass Carpoidea by ABEL (1920, p. 278), was performing some remarkable experiments in the modification of a quinquerradial symmetry into a new dorso-ventral asymmetry and a partial bilateral symmetry, and that some of them approach in general patterns to the 'dorsal' and 'ventral' shields of *Drepanaspis* among the heterostracous ostracoderms" (GREGORY 1936, pp. 320—321). Further GREGORY objected to "the tradition that the invertebrate ancestors of the vertebrates must necessarily have been bilaterally symmetrical and metameric forms moving in a cranio-caudal direction like worms and primitive arthropods" (l.c.). The significance of *Branchiostoma* as a true intermediate between vertebrates and invertebrates was denied and it was thought to have been "derived by degeneration and specialization from some of the known Palaeozoic chordates" (GREGORY 1936, p. 322), whereas the Heterostraci were supposed to be the initial vertebrate group.

It is evident that a hypothesis like this must have seemed strange to several scientists and cannot have won general acceptance.

There is one circumstance which may be worth mentioning in this connexion, if we consider that the Pelmatozoa are throughout marine. Recent investigators (ROMER & GROVE 1935 a, 1935 b; DACQUÉ 1935, pp. 374—375; ABEL 1942) have namely shown that the oldest vertebrates were not marine but are found in deposits of fresh and brackish waters.

The question of the origin of Chordonia can of course not be discussed here. But it may be recalled that the Deuterostomia — Enterocoelia comprise, besides the Chordonia and Echinodermata, only the Enteropneusta, Chaetognatha, and Tunicata. This does not speak in favour of the annelid theory of SEMPER-DOHRN. As to the rest, the present writer may restrict himself to referring to the papers of LÖNNBERG (1902), BARROIS (1924), TRETJAKOFF (1929; with an extensive list of references), GISLÉN (1930), and GREGORY (1936).





Text-fig. 3. *Echinospaerites aurantium* (GYLLENHAAL). Casts showing grooved impressions in the oro-anal area. o=mouth, g=gonopore, a=anus.  $\times 2$ . — A: RM Ec 3183. B: RM Ec 3182. C: RM Ec 3030. Västergötland.

of the anus (JAEKEL 1899, p. 126). This interpretation of the grooved impressions was accepted by BATHER (1913, p. 458, § 384). In spite of the probability of the theory thus presented, one cannot help wondering how so soft tissues as those of a mesentery could at all be traced after fossilization, though very seldom. There is also another hitch, pointed out by HECKER (1923, p. 29), viz. the branching of the lines in the region of the gonopore. Further it should be noted that, in a specimen of *Echinospaerites*, HECKER observed a system of crystalline ribs, circular in transverse section. Their extension over the theca was said to agree throughout with the course of the grooved impressions made known by JAEKEL and, therefore, must represent the same structures (HECKER 1923, p. 28). As for their nature it would be more natural to think that we have here to do with branched ducts, circular in transverse section, the signification of which is obscure, however (HECKER 1923, p. 29). And it must be acknowledged that the facts offered by HECKER are definitely not in favour of the septal theory.

ANGELIN (1872 a, Pl. 27, fig. 15) figured a specimen of *Sphaeronites pomum* (GYLLENHAAL) [RM Ec 2789] showing a peculiar system of sub-skeletal flattened or faintly keeled ribs branching and anastomosing (cf. our fig. 5 on Pl. 1 with ANGELIN's fig., which is rather inadequate). These structures, which could possibly be suspected to belong to the same category as those just mentioned, are distributed all over the body, though irregularly, under — or partly within? — the skeleton plates. In this case we have to consider the possibility that the structures in question are (postmortal?) changes caused by the activity of some unknown organism.

The orifices of the alimentary and reproductive system, and of the stone canal, often referred to as the "primary pores", which are all

or in part to be found in the wall of the theca in the Cystoidea, have been interpreted rather differently by different scientists, and the understanding of the true importance of the several openings has been gained by and by. To show this and to facilitate the use of the papers of certain older authors the table on p. 58 was compiled.

It is evident how — on the authority of BUCH — anus and gonopore (“ovarian aperture”) were confounded by several distinguished authors. The first to correct the mistake was F. ROEMER, according to statement by JAEKEL (1899, p. 137). The papers of ROEMER 1851 and 1852 were unfortunately not available to the present writer.

Whether the term “gonopore” or “parietal pore” is to be preferred, might not be of very great importance. Here the term “gonopore” has been adopted, being that generally used by authors writing in English. JAEKEL (1899, p. 143) recommended, however, the use of the term “parietal pore” as being more indifferent. This view was based on the assumption that this pore, the connexion of which with the genital function was recognized, acted in many forms contemporarily as a hydropore.

As pointed out by JAEKEL (1899, p. 128), the term “peristome” should strictly stand for the thecal opening usually referred to as “mouth”, in view of the fact that the radial extensions of the ambulacral system and radial nerves also passed into the theca through the oral opening. In the same way the “anus” should rightly be termed “periproct”, since the anus occupied only a part of the periproctal area.

The grooves extending radially from the mouth have been called “food-grooves”, “subvective grooves”, “ambulacral grooves”, or “ambulacra”. These terms seem to be about equally suitable. If we wish, however, to reduce the number of terms, the two first-mentioned should possibly be dropped in favour of “ambulacra” (or “ambulacral grooves”).

The interior of the theca practically never displays anything of the course of the alimentary canal or other features of visceral organization, this according to the experience of the present writer from all specimens examined by him and according to the statements of several investigators. The matrix usually contained in the theca does not — or at least not as a rule — reproduce the course of the alimentary canal, which is evident from the fact that in thin-sections orientated mutually in the same way, the interior of the theca has a rather varying appearance, where it is not quite filled up with matrix. This can be understood only by assuming either that the matrix did not pass into the theca until the viscera were destroyed or not until the process of destruction had advanced more or less. Besides, an irregular crystallization of the thecal walls plays sometimes a role for determining the shape of the interior actually visible.

|                       | Mouth                                                                        | Anus                                  | Gonopore                                                | Hydropore                                   |
|-----------------------|------------------------------------------------------------------------------|---------------------------------------|---------------------------------------------------------|---------------------------------------------|
| GYLLENHAAL 1772       | Os <sup>4</sup><br>(Rostrum inferius = peristomal projection) <sup>5</sup>   | Anus <sup>4</sup><br>Os <sup>5</sup>  | Anus <sup>5</sup>                                       | —                                           |
| HISINGER 1802 &c.     | Anus <sup>4</sup><br>(Rostrum inferius = peristomal projection) <sup>5</sup> | Os                                    | Anus <sup>5</sup>                                       | —                                           |
| WAHLENBERG 1821       | Os<br>(Rostrum) <sup>5</sup>                                                 | Anus<br>Os <sup>5</sup>               | Anus <sup>5</sup>                                       | —                                           |
| PANDER 1830           | (Stielöffnung = peristomal projection) <sup>6</sup>                          | Mund                                  | (This pore was noted, but its function was not settled) | —                                           |
| BUCH 1840 &c.         | Mund                                                                         | Ovarialöffnung <sup>7</sup>           | Analöffnung                                             | —                                           |
| EICHWALD 1840 &c.     | Bouche                                                                       | Orifice genital                       | Anus                                                    | —                                           |
| VOLBORTH 1846 &c.     | Mund                                                                         | Ovarialöffnung                        | Anus                                                    | Madreporenplatte?                           |
| FORBES 1848           | Mouth                                                                        | Ovarian orifice                       | Anal orifice                                            | —                                           |
| HALL 1852 &c.         | Mouth                                                                        | Ovarian aperture                      | Anal aperture                                           | —                                           |
| J. MÜLLER 1854        | Mund                                                                         | Genitalöffnung? <sup>7</sup>          | —                                                       | —                                           |
| BILLINGS 1858 &c.     | Ambulacral orifice <sup>8</sup>                                              | Mouth <sup>9</sup>                    | Anus                                                    | —                                           |
| LOVÉN 1867 &c.        | —                                                                            | Mun (mouth), also functioning as anus | Könsorgan (genital organ)                               | Madrepore?                                  |
| F. SCHMIDT 1874       | Ambulacralöffnung                                                            | Mund <sup>10</sup>                    | Afteröffnung                                            | —                                           |
| ANGELIN 1878          | Os                                                                           | Anus                                  | Apertura genitalis                                      | —                                           |
| BARRANDE 1887         | Bouche                                                                       | Ouverture ovarienne?                  | Anus?                                                   | Quatrième ouverture (Plaque madréporique?)  |
| S. A. MILLER 1889 &c. | Ambulacral orifice                                                           | Mouth                                 | (Sometimes: Anal opening)                               | Anal opening                                |
| CARPENTER 1891        | Mouth                                                                        | Anus                                  | Gonopore                                                | Hydropore                                   |
| HAECKEL 1896          | Mund (Osculum)                                                               | After (Anus)                          | Genital-Porus (Gonoporus)                               | Vierte Oeffnung (Hydroporus?)               |
| JAEKEL 1899 &c.       | Mund                                                                         | After                                 | Parietalporus                                           | Porus des primären Steinkanales (Madrepore) |
| BATHER 1900 &c.       | Mouth                                                                        | Anus                                  | Gonopore                                                | Hydropore                                   |



BILLINGS (1858 a, p. 19) expressed the fear that not "a single specimen retaining even a vestige of the soft parts will ever be discovered". And it is true that in the course of time only two specimens (of *Caryocrinites ornatus* SAY, from the State of New York) have been observed, in which the alimentary canal is directly visible within the theca, being preserved thanks to calcification of the gut-wall (cf. JAEKEL 1899, p. 135 seq.). But even where no direct evidence is present, the position and interrelation of the two endpoints of the alimentary canal — mouth and anus — give an idea of the extension of the gut. Further conclusions may be drawn from the distribution of the pore-rhombs, where such are developed (BATHER 1900, p. 58; 1913, p. 508, § 606), and by comparison with known forms. According to the investigations on the matter carried out by JAEKEL, the gut of the cystoids shows a close affinity to that of Crinoidea Camerata ("Cladocrinoidea") with regard to structure and course within the theca (JAEKEL 1899, p. 137).

Our information on the ontogeny of cystoids (and Paleozoic Pelmatozoa in general) is exceedingly poor. In 1922 BATHER published some notes on growth stages of *Orophocrinus stelliformis* (OWEN & SHUMARD), where the so-called var. *campanulatus* HAMBACH was demonstrated to represent the young of *O. stelliformis*. Recently there appeared two interesting studies, one by CRONEIS & GEIS (1940) on the ontogeny of the Blastoidea, and one by MOORE (1940) on early growth stages of Carboniferous microcrinoids and blastoids. In the first-mentioned paper the "first completely known larval stages of Paleozoic pelmatozoans, as represented by early growth sequences in two genera of late Mississippian blastoids, *Mesoblastus* and *Pentremites*" (CRONEIS & GEIS 1940, p. 345), were described. Since in these genera, though relatively dissimilar in mature state, the course of ontogenetic development was found to be essentially the same, it was inferred that the stages observed may be "characteristic of the class [i.e. subclass Blastoidea, acc. to the classification here adopted] rather than of any one genus" (l.c.). Critical comments upon this paper and further valuable

<sup>4</sup> In describing *Sphaeronites pomum* (GYLLENHAAL).

<sup>5</sup> In describing *Echinospaerites aurantium* (GYLLENHAAL), in the case of HISINGER a few other forms too.

<sup>6</sup> The true base was interpreted as anus.

<sup>7</sup> In *Caryocrinites*, which was referred to the Crinoidea, the true anus was interpreted as mouth.

<sup>8</sup> BILLINGS (1870, p. 256; 1871, p. 158) wished not to deny the possibility that this aperture might represent the mouth, though the opinion advanced by him in 1858 seemed to him the more probable one.

<sup>9</sup> This opening was thought in some species to have served likewise as anus (i.e. in species where the aperture now interpreted as gonopore was not detected).

<sup>10</sup> "Die Deutung der Klappenpyramide (hier und bei andern Cystideen) als Mund, wie ich bei meiner letzten Arbeit (Miscellanea silurica II) mit LOVÉN gegen VOLBORTH annahm, ist mir gegenwärtig wieder zweifelhaft geworden" (F. SCHMIDT 1880, p. 4).

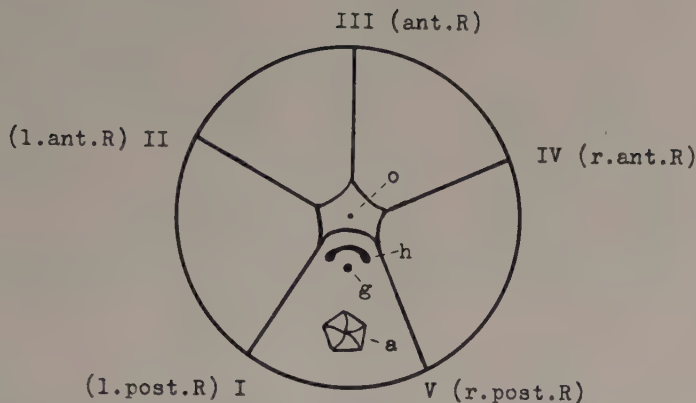
observations on early growth stages were given by MOORE (1940), who also (p. 572) explained the several difficulties connected with ontogenetic researches in fossil echinoderms. References were made to the very limited literature of immature crinoids.

Noticeable investigations on the ontogenetic-phylogenetic development of the stomodaeum of certain pelmatozoans seem to have been performed by G. DELPEY (1942 a). The paper in question was unfortunately not available to the present writer.

**O r i e n t a t i o n o f t h e t h e c a.** The rules for the orientation of a crinoid calyx were set forth by BATHER 1900 (pp. 109—110) and have been applied to the cystoid theca too. Thus it has to be placed mouth upwards, the anal interradius facing the observer. Though downwards in a figure (i.e. nearest the observer), the interradius containing the anus had of course to be termed "posterior", and the radius opposite to it (i.e. right away from the observer) "anterior". This change of anterior and posterior in relation to the natural conception of the observer may give rise to confusion, as emphasized by JAEKEL 1918 (p. 8). An example of this is afforded by certain descriptions of cystoids delivered by READ 1917 (cf. also BATHER 1918 b, figs. 1—4). Designations and symbols for the radii and interradii, based on the principles "anterior" and "posterior", respectively "antero-lateral" and "postero-lateral", and "right" and "left", were introduced by BATHER 1900 (p. 110), right and left corresponding to the right and left of the observer.

To avoid this rather complicated and heavy system and the inconveniences connected with it, it seems to be advisable to accept the indifferent symbols used by JAEKEL (1895 seq.). According to JAEKEL each radius is indicated by one of the Roman numerals I—V. As a basis to start from are taken the hydropore and gonopore, which, if not obliterated, were invariably connected with the dorsal vertical mesentery, the "parietal septum" (JAEKEL 1899, p. 104; 1918, p. 93. Cf. also p. 55 above). Thus their position is constant, whereas this is not true of the anus. The radius to the left of the pores mentioned is symbolized by the numeral I. The remaining radii are counted in clock-wise ("solar") direction (cf. text-fig. 4), so that the hydropore and the gonopore come to lie in the interradius V—I (which is also in many cases anal interradius). This system advanced by JAEKEL (cf. especially 1918, pp. 6—8) is undoubtedly the fittest in the case of the Cystoidea (accepted also for the Edrioasteroidea by BASSLER 1935 and 1936, who used, however, Arabian figures) and is suitable for all echinoderms for the purpose of mutual comparison. Yet BATHER's system was recommended by W. E. SCHMIDT (1923, p. 144) for the Crinoidea.

For a table comparing the systems of BATHER, JAEKEL, and others, the writer begs to refer to BATHER 1900, p. 110 (cf. also our text-fig. 4, in which



Text-fig. 4. Orientation of the theca in the Cystoidea. Within brackets: symbols used by BATHER. o=mouth, h= hydropore, g=gonopore, a=anus.

the symbols used by BATHER for the radii are indicated within brackets; the symbols for the interradii were excluded in the figure but should be written I—II, &c.).

A very useful epitome of terms for certain organs, the planes of symmetry, &c. was presented by BATHER 1918 b (pp. 508—511). We also owe to BATHER the elaboration of a system of symbols for the skeleton elements employed in the technical description of Pelmatozoa. These symbols were intended in the first place for crinoids (cf. the tables in BATHER 1893, pp. 17—18, and 1900, p. 143), but were used in applicable parts also for other pelmatozoans. A revised list of symbols for crinoid parts was published by MOORE & LAUDON 1941 (p. 421). The symbols recommended there agree with those currently used by numerous paleontologists. The present author agrees with MOORE & LAUDON in writing the symbols in capital italics and in indicating pluralization by duplication of the symbol, or, in composed terms, of its second member. The following symbols will be used:

*O*=oral, *OO*=orals [=deltoids of authors]<sup>11</sup>

*R*=radial, *RR*=radials [=radiolateralial (*l'*, *L'*) JAEKEL]<sup>12</sup>

*L*=lateral, *LL*=laterals [=mediolateralial (*l'*, *L'*) JAEKEL]<sup>12</sup>

*IL*=infralateral, *ILL*=infralaterals [=l, *L*, JAEKEL]

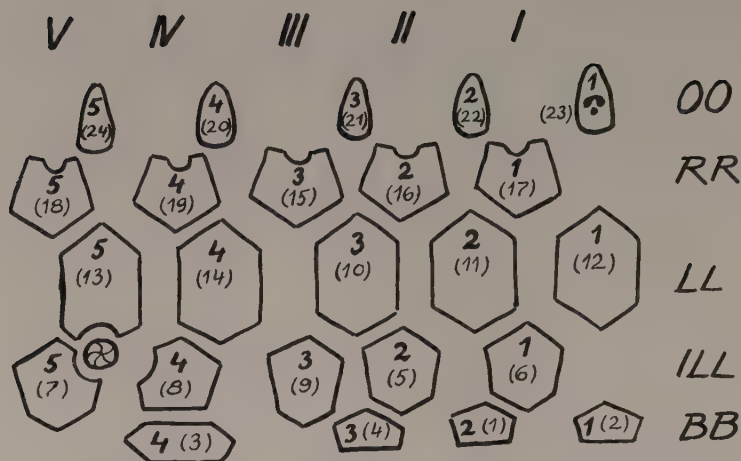
*B*=basal, *BB*=basals.

It should be noted, however, that the homology between the different plates in Cystoidea and Crinoidea may not be taken for granted.

<sup>11</sup> According to BATHER (1900, pp. 100, 143) the term "oral" (noun) is synonymous with "deltoid" (symbolized by  $\triangle$  or  $D$ ) used by himself and others.

<sup>12</sup> In the revised list of MOORE & LAUDON (1941, p. 421) *R* symbolized "radial" as well as "right", and *L* was taken as symbol of "left".





Text-fig. 5. Numbering of the thecal plates in the Hydrophoridae, according to JAEKEL and, within brackets, according to BATHER; symbols of circlets modified. Diagram showing the supposed archetype of the Glyptocystitida. (Combined after BATHER 1913, text-figs. 36—37, modified).

BATHER did not use special denominations for the different cycles of the lateral plates of the theca and — following FORBES (1848) — indicated the single plates by figures from a running series, beginning in the basal cycle. JAEKEL (1899, pp. 198—200) introduced a term for each of the lateral cycles. This method was deemed by the present writer to be useful, the single plates being denoted with figures of a series beginning in each cycle with 1 in radius I, respectively interradius V—I, and proceeding in clockwise direction (cf. text-fig. 5). The mode of counting mentioned and the (modified) symbols of JAEKEL's were, therefore, adopted here.

## Systematic Survey of Swedish non-Crinoid Pelmatozoa.

In preparing this part of the present paper, the writer often had occasion to think over a passage by R. RICHTER, quoted below, which anyone should keep in mind, who may happen to read this section — as well as any paper dealing monographically with a group of organisms. RICHTER says: —

“Dem Schreiber ist das Festhalten von kleinen und sich bei der nächsten Art vielleicht wiederholenden Eigenschaften eine lästige Mühe. Aber er muss bedenken, dass er nicht für sich sondern für den Benützer schreibt. Diesem aber, der die Arbeit nicht im Zusammenhang liest, sondern mit einem Griff die gesuchte Einzel-Angabe finden will, nützt nur Vollständigkeit und Ordnung.”

In this connexion it may be emphasized that taxonomists owe a good deal to Prof. RICHTER for his indefatigable efforts to standardize also the, so to speak, technic side of scientific publication and to elucidate and vindicate the international rules of nomenclature. The present writer has profited very much by his ‘Einführung in die zoologische Nomenklatur durch Erläuterung der internationalen Regeln’.<sup>1</sup>

At the compilation of the lists of synonyms of the species it was not deemed necessary in this case to use a system of symbols recommended by RICHTER. The reason for this is that the lists, owing to their brevity, are easy to penetrate also without explanatory symbols. It was thought useful, however, to indicate, by italicizing the numbers of certain dates in the list of synonyms, that the paper quoted does not bring a description or figures of the species but only a mentioning and thus does not contribute to the knowledge of the morphology of the species in question.

In giving the stratigraphic range of Swedish genera and species, the different portions of the Ordovician and Silurian systems are referred to as Lower, Middle, and Upper. These divisions are arbitrary. The terms are used thus: — Lower Ordovician = the Ceratopyge series, Middle Ordovician

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<sup>1</sup> Frankfurt a. M. 1943 (Senckenb. Naturf. Gesellsch.).

=the *Asaphus* and *Chasmops* series, Upper Ordovician = the *Tretaspis* series, Lower Silurian = strata of Llandoveryan (Valentian) age, Middle Silurian = strata of Wenlockian age, Upper Silurian = strata of Ludlovian age.

## Material and Methods.

### Material available. State of Preservation.

The present author has had the favour to study the bulk of the material of Swedish fossil *Pelmatozoa* non-*Crinoidea* hitherto collected and, for comparison, the material from foreign countries kept in the State Museum of Stockholm. The museums from which collections have been placed at the author's disposal were mentioned in the preface.

The critical elaboration is rendered difficult through the generally sparse occurrence of these organisms. Good specimens are very rare, as observed e.g. already by BILLINGS (1858 a, p. 10) and further pointed out by JAEKEL (1899, p. 5), who might have had in hand at one occasion a greater material than any other student of cystoids. Also BATHER 1900 (p. 40) made the same statement.

Of Swedish species a few are exceedingly abundant in certain strata of the Middle and Upper Ordovician. Well-preserved specimens are found relatively seldom, however. Among those common species *Sphaeronites pomum* (GYLLENHAAL) and *Echinospaerites aurantium* (GYLLENHAAL) are first to be mentioned. Also *Heliocrinites granatum* (WAHLENBERG) and *Caryocystites angelini* HAECKEL are met with frequently at certain localities. The rest are more or less rare (cf. JAEKEL 1899, p. 145).

The state of preservation is in many cases less favourable to a closer investigation of the specimens. In all specimens in which the interior was made visible through the preparation of thin sections all traces of the internal organization were unfortunately totally obliterated. It may be mentioned, however, that — under especially fortunate conditions — the soft portions of the alimentary canal may be traced, as appears from two specimens of *Caryocrinites ornatus* SAY from Lockport in the State of New York, examined by JAEKEL (1899, p. 135). It is clear that the original structures of the skeleton plates are considerably more apt to be preserved in a recognizable state. At the crystallization, as is well known, each skeletal element in *Pelmatozoa*, as in other fossil echinoderms, gives rise to an individual calcite crystal, the axis of which is coincident with the organic axis. Each plate thus presents itself as a perfectly cleaving calcite fragment.



The name "crystal-apple" attached to the cylindrical bodies of certain cystoids is of course due to the centripetal growth of the calcite crystals on the inner side of the test. This mode of crystallization, peculiar to the echinoderms (cf. yet p. 48 above), is initiated by the primary orientation of the calcium carbonate of the skeletal elements. For the calcium carbonate secondarily supplied and absorbed by the reticular stroma of the skeleton crystallizes in continuity with the calcite of the original structures. During this process the test often became thicker, but the details of structure and surface sculpture were preserved. — Not seldom are the specimens in hand as internal moulds.

In a few cases the mode of preservation differs from that usually found. From the Lower Chasmops limestone of Böda Harbour, Öland, there are two specimens, probably belonging to *Sphaeronites globulus* (ANGELIN), in which the calcite is replaced throughout by pyrite [RM Ec 5769 (HISINGER collection); RM Ec 4371]. In this limestone, which is on the whole rather pure, the author observed at a visit to the locality in question in 1942 scattered lumps of pyrite, possibly growing from a nucleus formed by some fossil fragment. Further some pyrite (here observed closely associated with a specimen of *Haplosphaeronis*) is present in the Middle Ordovician so-called Cystoid shale of Scania, and in the Staurocephalus shale (Upper Ordovician) of Scania, where pyrite grains were seen to impregnate the shell of a *Helio-crinites* n. sp. (referred to as *Caryocrinites* sp. by TROEDSSON 1918, p. 21; both specimens mentioned in LM). As a general statement it may be said, however, that cystoids seem to be unfamiliar to pyrite-bearing sediments, or, in other words, these organisms did not thrive in the H<sub>2</sub>S-rich milieu indicated by abundant pyrite. In this respect the Cystoidea coincide with Echinoidea but differ from Crinoidea and Stellerioidea which are not seldom pyritized (DEECKE 1915, p. 14).

Internal moulds of *Echinosphaerites*, occurring in the Kinnekulle Mountain in a hard, splintery, lime-free rock of metamorphic appearance are sometimes quite silicious. This is the case e.g. in specimens from Ekberget [RM Ec 3079 &c.].

In the RM collection there are a few specimens of *Echinosphaerites* from Vika, Dalarna, which have been impregnated secondarily with asphalt [RM Ec 2217—2219]. The same was observed in a specimen of *Haplosphaeronis* from Kallholn, Dalarna [RM Ec 1847], and a specimen of *Eucystis* from Lissberg, Dalarna [RM Ec 2048].

On the whole it must be stated that the preservation of the Swedish non-crinoid pelmatozoans is as a rule not very favourable and decidedly inferior to that of e.g. Estonian fossil material.

### Methods used at the Preparation and Examination of the Material.

The specimens present in the collections at the author's disposal are as a rule weathered out from the rock. Where this is not the case, the matrix, as wanted, was removed from the specimens with the aid of a modified dental mallet of ARNELL's construction. In certain instances the task of preparing was rather delicate because of the fragility of the plates and thecal appendages.

In the examination of the material under the binocular ( $\times 3.5-32$ ) a pointolite lamp served as source of illumination.

To make sutures of plates and finer details of pores &c. to stand out as clearly as possible, attempts were made to stain the objects. CRONEIS & GEIS (1940, p. 346), at their study of larval blastoids, had found, after considerable experimentation, that methylene blue served the purpose tolerably well. According to the author's experience neither methylene blue, nor alizarine, which was also tried, work very well in the wanted direction, since the necessary degree of differentiation is not obtained. A far better result gave certain refracting liquids. Such were successfully used at the photographing of the specimens. Benzol (recommended by JACKSON 1912, p. 23, for Echinoidea), xylol, glycerine (successfully used by W. E. SCHMIDT 1934, p. 13, in photographing fossil Crinoidea), and alcohol, proved about equally suitable. The last-mentioned liquid being nicer to handle, it was usually preferred.

Coating with ammonium chloride sublimate proved very serviceable in photographing strongly and (or) unevenly coloured specimens.

Etching with diluted hydrochloric acid rendered good result in making clear the pore-system of *Echinosphaerites*, in which an epithek covering and concealing the pores is present. The method was made use of previously by e.g. JAEKEL (1899, p. 73) and by ORVIKU (1927).

Trials to obtain collodium imprints of skeleton structures for microscopic study did not meet with noteworthy success.

Thin sections were prepared of many specimens, but in no case indisputable traces of the alimentary canal or other internal organs were left. The pore system of the thecal plates could, of course, be studied in the sections.

The photographic pictures of specimens figured by preceding authors are usually orientated in the same way as the original figures in order to make comparison easier. — The sutures of plates were sometimes lined with pencil directly on the specimens.

## Subphylum **Pelmatozoa** LEUCKART 1848.

### Class **Eocrinoidea** JAEKEL 1918?

#### Genus ***Bockia*** HECKER 1938?

#### ***Bockia*?** sp.

Pl. 2, fig. 10.

**Locality:** — Fjäckå, Dalarna.

**Stratum:** — Chasmops limestone, Middle Ordovician.

**Material:** — A piece of rock with several plates, partly connected [RM Ec 2215].

**Remarks:** — The specimen here concerned seems to have had a sac-shaped theca, of which about a dozen plates are visible, many of them being very fragmentary. Since the theca is badly crushed, no definite opinion of its original shape can be given, however. The height might have been at least 4—5 cm.

The plates seem to have been as a rule hexagonal. They are large, thin, flattened or slightly convex. The approximate measurements of a couple of plates is 15×13 mm. The plates are not pierced by any pores, but their surface is ornamented with scattered tubercles, some of which have a minute pit in the top. Between the tubercles the test is granulated very finely, which becomes visible only at a power of at least ×15. A concentric ornament can be traced in some plates.

It is obvious that the rests here described are not in such a state of preservation as to be determined safely. The reason why they were here tentatively referred to the Eocrinoidea is the similarity — rather striking indeed — between the plates of this form and certain species of *Bockia* figured by HECKER 1940. In the first place this is true of *Bockia cucumis* HECKER 1940 (Pl. 8, fig. 6), which was described as follows: — “Theka sackförmig, die Anzahl der Platten nicht bedeutend; sie sind gross, erreichen 10—12 mm im Durchmesser; Oberfläche der besterhaltenen Platten sehr fein und dicht granuliert, ausserdem sind auf ihr scharf ausgeprägte Körner nicht dicht verstreut” (HECKER 1940, p. 71). As far as discernible, the given characters hold good of our specimen too, only that the dimensions of the plates are somewhat greater.

The stratigraphic range of the genus *Bockia* (four species were described by HECKER) is B<sub>2</sub>—C<sub>3</sub> of the East Baltic area. *Bockia cucumis* is confined to stage C<sub>3</sub> in Estonia, which is equivalent to the upper part of the Lower Chasmops limestone.



The lack of thecal pores excludes the present specimen from the Cystoidea. As just emphasized its position cannot be stated definitely, however. But besides the resemblance in plate habit to *Bockia* we may point at the following features suggesting the eocrinoid nature of this fossil: — the supposed sack-like shape of the body, the irregularity in arrangement of plates, and the relative thinness of the plates.

If the above reasoning can be trusted, a certain interest is connected to this species, which would then be the only eocrinoid known as yet from the Swedish series of strata.

### Class **Cystoidea** BUCH 1846, emend. JAEKEL 1918.

#### Subclass **Hydrophoridea** ZITTEL 1903.

#### Order **Rhombifera** ZITTEL 1879, emend. BATHER 1899.

JAEKEL (1899, 1918) divided the Rhombifera ("Dichoporita" JAEKEL) into two groups: — Regularia and Irregularia, the pentamerism of the last-mentioned being disturbed by the insertion of additional plates. For reasons explained by BATHER (1913, p. 427, § 265 seq.), these divisions — and in particular the names given to them — are very inappropriate. In recognition of the close relationship between the families comprised in the Regularia, BATHER (1913, p. 433, § 280 seq.) yet proposed to group them in a superfamily, Glyptocystidea, corresponding to the family Glyptocystidae of BATHER 1900. This arrangement will be adopted here.

The order in which the families are ranged below is according to the system of JAEKEL 1918.

#### Superfamily **Glyptocystitida** (BATHER 1913) n. nomen.

##### Family **Cheirocrinidae** JAEKEL 1899, emend. BATHER 1913.

##### Genus **Cheirocrinus** EICHWALD 1856.

*Genotype*: — *Cyathocrinus penniger* EICHWALD 1842.

*Synonyms*: — See BATHER 1913 (p. 434, § 286).

The genus was discussed at some length by BATHER (1913, p. 434, § 287 seq.) and a fresh diagnosis was given.

*Regional distribution*: — Sweden (Middle Ordovician), USSR and Estonia (Middle Ordovician), ? France (Middle Ordovician), Norway

(Middle Ordovician), N. America (Middle Ordovician), Burma (Middle Ordovician),<sup>1</sup> Bohemia (Middle and Upper Ordovician) Britain (Middle? and Upper Ordovician), Greenland (Upper Ordovician).<sup>2</sup>

Stratigraphic range: — Middle—Upper Ordovician.

*Cheirocrinus holmi* n. sp.

Pl. 2, fig. 11. Text-figs. 6—7.

1882 *Glyptocystis*. — HOLM, p. 68.

1888 *Glyptocystis* sp. n. — LINDSTRÖM 1888 a, p. 8.

1899 *Chirocrinus ornatus* EICHWALD 1860 (ex parte). — JAEKEL, p. 220.

Derivation of name: — The species is named after the distinguished paleontologist G. HOLM (1853—1926), who collected the only specimen known.

Holotype: — RM Ec 5028.

Type locality: — Closely N of Äleklinta,<sup>3</sup> Öland.

Type stratum: — A bed of green limestone bearing *Megalaspis planilimbata*, *Symphysurus breviceps*, &c., lowest member of the *Asaphus* series, Middle Ordovician.

Material: — One imperfect specimen, the holotype.

Diagnosis: — A species of *Cheirocrinus*, the thecal plates of which are ornamented with strong single axial ridges, which dilate in part peripherally, being provided with transverse rugae or ridges; pectinirhombs conjunct.

Description: — The general shape of the theca cannot be deciphered from our specimen, the plates being largely disjointed. As a matter of course the arrangement into cycles of the elements of the thecal skeleton also becomes obscure, the identification of most plates being impossible to perform. The plates are thick, mainly hexagonal; in the only two plates entirely exposed the long axis is 14 mm and the short one 9 mm, respectively 11 mm and 9 mm.

Surface structures of stereom. Six (or in cases less than six?) strong single axial ridges of each thecal plate visible, except *B* 2, are very prominent, two of them — in the plates exposed those of the long axis — being especially well developed, dilating considerably towards the margin, where they meet a ridge originating from the umbo of an adjacent plate. They also increase considerably in height from the umbonal area (text-fig. 6). The back of these ridges is more or less rounded and provided with 6—7

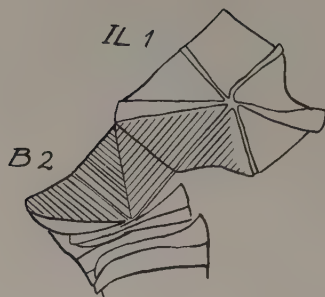
<sup>1</sup> REED 1906 (p. 26).

<sup>2</sup> TROEDSSON 1928 (p. 105).

<sup>3</sup> Wrongly written as "ALLE's Klinta" by JAEKEL (1899, p. 220).



Text-fig. 6.



Text-fig. 7.

Text-fig. 6. *Cheirocrinus holmi* n. sp. [RM Ec 4170]. Lateral view of a thecal plate in the holotype (the plate lying to the right in Pl. 2, fig. 11).  $\times 3$ . — Öland: Åleklinta.

Text-fig. 7. *Cheirocrinus holmi* n. sp. [RM Ec 4170]. Thecal plates in the holotype (IL 1—B 2) showing conjunct pectinirhombs.  $\times 2$ . — Öland: Åleklinta.

rugae or ridges. The portions between the axial ridges — where not occupied by pectinirhombs — seem to be smooth.

**Pores of the thecal plates.** On account of the imperfect state of preservation of the theca, the distribution of the pectinirhombs cannot be stated in general. But the plates lying close to the proximal portion of the stem (by analogy with other species it may be inferred that those plates are B 2 and IL 1; cf. the description of *Cheirocrinus leuchtenbergi* below) demonstrate clearly that the pores, or at least part of them, are arranged in conjunct pectinirhombs (text-fig. 7) with fine pore-slits.

Nothing is visible to show the structure of the ambulacral system, nor of the primary pores.

The stem is rather well preserved, being of the ordinary shape in *Cheirocrinus*; 24 columnals are present in our specimen, the number being a little less than in a complete state. The stem was evidently in possession of strong muscles so that the stem segments could be drawn together concertina-like.

**Discussion:** — As appears from the list of synonyms compiled above, this species, which was collected in 1882 by G. HOLM, was first referred to as *Glyptocystis* without any specific determination. In his 'List of the fossil faunas of Sweden' LINDSTRÖM (1888 a, p. 8) recognized it as a new species. JAEKEL (1899, p. 220) identified the Ölandian form with *Cheirocrinus ornatus* EICHWALD.<sup>4</sup> A comparison with that species as figured

<sup>4</sup> The age of the Russian species, from Pulkova S of Leningrad, cannot be fixed definitely, but it might possibly be fairly synchronous with the Swedish form. It is true that BASSLER (1911, p. 20) and SCUPIN (1928, p. 172) listed *Cheirocrinus ornatus* as originating from the stage B<sub>3</sub> (the so-called Vaginatum limestone), which corresponds to the



by EICHWALD (1860, Pl. 32, fig. 2 c) shows that there is, indeed, a rather great general similarity between the two forms with regard to the stereom structures of the thecal plates. But whereas in our species only two axial ridges of each plate are dilated distally, four of them have that shape in the plate figured by EICHWALD. By far a more important difference is that the pectinirhombs are conjunct in the present species but disjunct in *Cheirocrinus ornatus*. In respect of the structure of the pectinirhombs *Cheirocrinus holmi* agrees with the East Baltic *Ch. atavus* JAEKEL and *Ch. giganteus* LEUCHTENBERG (both of Middle Ordovician age, the former occurring, according to SCUPIN 1928, p. 172, in stage B<sub>2</sub>, the latter in B<sub>3</sub>), and the Scottish *Ch. constrictus* BATHER (Upper Ordovician). From all of them it differs by the strong axial ridges. According to JAEKEL (1899, pp. 220—221) all other species known up to then have disjunct pectinirhombs. Contrary to this statement BATHER (1913, p. 440, § 302) observed that in *Cheirocrinus alter* JAEKEL the rhombs of R 5—R 1 and R 1—R 2 are conjunct, as appears from fig. 8 of JAEKEL's Pl. 11. A thorough examination of the holotype of *Cheirocrinus leuchtenbergi* (ANGELIN) reveals that conjunct pectinirhombs are present in that species, too (cf. the description below). From both species mentioned *Cheirocrinus holmi* is easily distinguishable by the characteristic development of the axial ridges of the plates, a feature which, moreover, makes it impossible to be mistaken for any species but *Cheirocrinus ornatus*.

*Cheirocrinus holmi* is the oldest cystoid known as yet from Swedish series of strata and is one of the earliest representatives of its genus. Only *Cheirocrinus ornatus*, as just mentioned, and *Cheirocrinus* (?) *langedocianus* THORAL (1935 a, p. 115), originating from a series at the very base of the Arenigian in the Montagne Noir, might have appeared tolerably synchronously with our Swedish species. Therefore, it would of course have been of a special interest to get a detailed knowledge of these old Rhombifera. In spite of a very intense searching at the type locality and in equivalent beds at other localities in Öland, the present writer did not succeed, however, to supply additional material.

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Asaphus limestone of Sweden. JAEKEL (1899, p. 220) gave the horizon "unterster Vaginatenkalk". But it is not improbable that the term "Vaginatenkalk" was used in the sense of Orthoceratite limestone, which is, strictly, a wider conception applying to a series of strata of the Swedish Ordovician corresponding to B<sub>2</sub>—C<sub>1γ</sub> of the East Baltic area. For JAEKEL stated that in the Berlin museum there is an isolated plate of *Cheirocrinus ornatus* from the "Glaukonitkalk" at Leningrad. According to ÖPIK (1930, table facing p. 48), the Glauconitic limestone, or B<sub>2a</sub>, is in part an equivalent of the zone of *Megalaspis planilimbata* in Sweden. The type stratum of the Russian species might, therefore, fall in a horizon corresponding to B<sub>IIα</sub> (zone of *Asaphus priscus* and *Megalaspis planilimbata*) of Estonia. — The text of the original description (EICHWALD 1860, p. 647) gives no conclusive information about the stratigraphic position ("Calcaire à *Orthocératites*").

Regional distribution: — Sweden, Öland: Äleklinta.

Stratigraphic range: — Planilimbata limestone (oldest zone of the Asaphus series), Arenigian.

*Cheirocrinus leuchtenbergi* (ANGELIN 1878).

Pl. 2, figs. 12—14. Text-figs. 8—9.

1878 *Glyptocystis Leuchtenbergi* ANG. — ANGELIN 1878 a, p. 32, Pl. 12, figs. 13—15.

1888 *Glyptocystis Leuchtenbergi* A. — LINDSTRÖM 1888 a, p. 13.

1890 *Glyptocystis* (*Leuchtenbergi* ANG.?) [sic!], — MOBERG, p. 13.

1899 *Chirocrinus Leuchtenbergi* ANGELIN sp. — JAEKEL, p. 220.

1906 *Glyptocystis* (*Leuchtenbergi* A.?). — WIMAN 1906, p. 104.

Lectotype: — RM Ec 3295, the specimen figured by ANGELIN (1878 a), Pl. 12, fig. 13.

Type locality: — Husbyfjöl,<sup>5</sup> Östergötland.

Type stratum: — Greenish grey limestone (Expansus limestone) of the Asaphus series, Middle Ordovician.

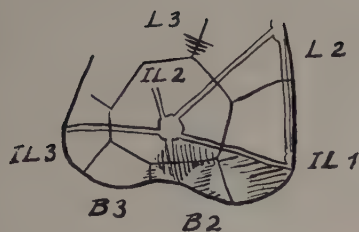
Material: — Besides the lectotype, which shows part of the basal portion of the theca, detached plates or plate-fragments probably referable to this species are present in some twenty samples [RM and LM]. A few of these contain a considerable number of scattered skeleton fragments.

Diagnosis: — A species of *Cheirocrinus*, in which pectinated demirhombs are present in *B* 1—*B* 2, *B* 2—*B* 3, and complete pectinirhombs in *IL* 1—*B* 2 (mainly disjunct), *B* 2—*IL* 2, and *L* 2—*L* 3 (conjunct) [the fragmentary state of the material available does not admit knowledge of the distribution of rhombs in the rest of the theca]; axial ridges single, well-defined, usually not dilating very much peripherally and not provided with transverse rugae; the opening for the stem relatively small, occupying about a third of the diameter of the base surface.

Description of the lectotype: — The general shape of the theca cannot be determined safely from the preserved fragment. It might be inferred, though, that the theca had the shape of a somewhat compressed pyramid. The base surface is flat and slightly impressed.

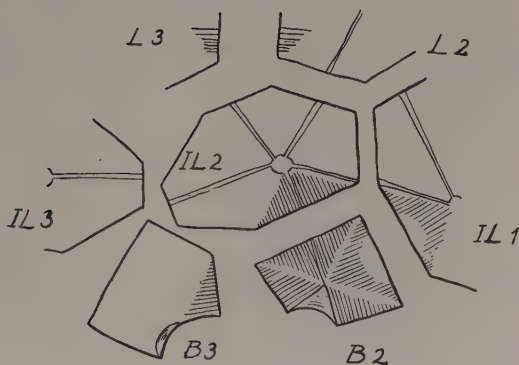
The arrangement of the plates of the exposed portion of the thecal skeleton should be elucidated by text-fig. 8, which corresponds tolerably to ANGELIN's Pl. 12, fig. 13 and our Pl. 2, fig. 12. A comparison will prove at once that the construction of the theca is in no way apparent from ANGELIN's figure. The sutures between the plates are namely not indicated, because of which the observer gets the idea that the portion represented in the figure consists of one plate only. Nor are the rhombs reproduced correctly.

<sup>5</sup> The locality-name "Husbyfjöl" of older literature and labels refers to the quarries at Västana (Borensberg).



Text-fig. 8.

Text-fig. 8. *Cheirocrinus leuchtenbergi* (ANGELIN), showing arrangement of plates in the lectotype [RM Ec 3295] (to be compared with Pl. 2, fig. 12). Nat. size. — Östergötland: Husbyfjöl.



Text-fig. 9.

Text-fig. 9. *Cheirocrinus leuchtenbergi* (ANGELIN). Analysis of the theca in the lectotype [RM Ec 3295].

An analysis of the theca, as far as preserved, is shown in text-fig. 9. The orientation given is not directly evident from the specimen but could be reconstructed by analogy with better known forms and is further confirmed by the fact that the periproct is not to be traced in the exposed skeleton area. In the first hand, however, we are induced to accept the orientation here proposed by considering the distribution of the pectini-rhombs. Such were stated by BATHER (1900, p. 63) to be constant on *B 2*—*IL 2* and *IL 1*—*B 2*, with demi-rhombs on *B 2*—*B 3* and *B 1*—*B 2* (the symbols used by BATHER were changed for the symbols here adopted). If we presume that the plates present in the lectotype are those indicated in the diagram, then the location of the rhombs is exactly as asserted by BATHER. The conclusion from this is not affected by the fact that the general statement concerning the constancy of the distribution of the rhombs has later proved incorrect by the additional evidence of a few species (BATHER 1913, pp. 438—439, § 298).

The shape of the different plates is shown approximately in the text-figures. The plates integrating in the base-surface are bent almost at right angles.

The diameter of the base is about 27 mm. Otherwise no measurements of the theca could be supplied. The long diameter of *IL 2* is 16 mm and the short one 10 mm.

Surface structures of stereom. The plates of *ILL* and *LL* have a well-marked umbo, from where thread-like single axial ridges radiate, each to proceed to the umbo of an adjacent plate. In the only plate fully



exposed, five well-defined ridges originate from the umbo. One further ridge, between *IL* 2 and *B* 3, is merely indicated. The back of the ridges is smooth. This is also true of those portions between the ribs in which no pectinirrhombs are developed.

**Pores of the thecal plates.** Distribution and development of the pectinirrhombs were already mentioned in the diagnosis and in the account of the orientation of the theca. All pectinirrhombs visible are conjunct but for *IL* 1—*B* 2, which is not, however, perfectly disjunct, only the central area being bridged over with stereom.

**Ambulacral system and primary pores** remain unknown.

Nothing is preserved of the stem. The opening for it in the thecal base-surface seems to be relatively small in comparison with that of most other species of *Cheirocrinus*. Its diameter is 9 mm, which is a third of the diameter of the base.

**Remarks on the typoids:** — The specimen [RM Ec 3300] figured by ANGELIN (1878 a), Pl. 12, fig. 15 (=our Pl.-fig. 2: 13), has to be looked upon as a paratypoid of *Cheirocrinus leuchtenbergi*, whereas the Norwegian specimens in ANGELIN's Pl. 12, figs. 16, 16 a, 17, 17 a—c, were removed by JAEKEL (1899, p. 221) and transferred to his species *Cheirocrinus nodosus*, to which they might not belong, however (cf. below, the following species).

The paratypoid might represent a basal plate, probably *B* 2. The rest of the material available consists of isolated or scattered plates, which do not seem to add very much to our knowledge of the morphology of the species. A good deal of them show one half of a perfectly disjunct pectinirrhomb, others bear the half of a conjunct rhomb. An especially large and sculptural plate is figured on Pl. 2, fig 14. The long diameter measures 27 mm and the short one 20 mm. The umbonal apex is elevated 11 mm over the lowest margin of the plate. The axial ridges are very strong and some of them dilate a little towards the periphery. — One slab [RM Ec 3139], from Våmb by Skövde, contains circular columnals.

**Discussion:** — As mentioned above (p. 71), conjunct pectinirrhombs are known to be present only in *Cheirocrinus holmi*, *Ch. atavus*, *Ch. giganteus*, *Ch. alter*, *Ch. constrictus*, and the species under discussion. Besides in the latter form, thread-like single axial ridges are met with in *Ch. atavus*, *Ch. giganteus*, and *Ch. constrictus*. The last-mentioned differs from all other species of the genus in having the basal rhombs restricted to *B* 2—*IL* 2 (BATHER 1913, p. 448, § 333). The two remaining East Baltic species have all pectinirrhombs conjunct. *Ch. atavus* may further be separated by its small size and the occasional appearance of radially arranged tubercles between the axial ridges (JAEKEL 1899, p. 219). Regarding *Ch. giganteus* it may be said that it is hard to get an exact idea of its morphology from the

information available in literature (LEUCHTENBERG 1843, p. 19; F. SCHMIDT 1874, p. 23, ex parte; JAEKEL 1899, p. 220). It seems, however, to be rather closely related to the Swedish species, irrespective of all pectinirhombs being conjunct, differing chiefly by its large dimensions. *Ch. giganteus* occurs in the stage B<sub>3</sub> (SCUPIN 1928, p. 172), which is equivalent to the type stratum of *Ch. leuchtenbergi*.

**Regional distribution:** — Sweden, Östergötland: Husbyfjöl-Västana, Kungs Norrby, Borghamn. — Närke: Lanna. — Västergötland: Våmb by Skövde, Österplana on Kinnekulle. — Dalarna: Stenberg by Orsa, ? Fjäckå (cf. below). — Öland (mentioned, with a mark of interrogation, by MOBERG 1890, p. 13, locality not indicated; the statement was repeated by WIMAN 1906, p. 104).

**Stratigraphic range:** — All specimens, except those from Fjäckå, originate from the same horizon as the lectotype, viz. the *Expansus* (or Lower *Asaphus*) limestone in the middle of the *Asaphus* series, Upper Arenigian. The specimens from Fjäckå [RM Ec 2306—2307; specimens in LM], Lower *Chasmops* series (Upper Llandeilian), represented by fragmentary plates, seem to belong to *Cheirocrinus leuchtenbergi* but cannot be determined quite safely. It may be remarked that LINDSTRÖM (1888 a, p. 13) mentioned the species from the "Upper grey Orthoceratite limestone" [=Schroeteri (Chiron) limestone, uppermost *Asaphus* series], which might be due to a mistake, however. It was namely not listed from the »Lower grey Orthoceratite limestone" [=*Expansus* (Lower *Asaphus*) zone].

### *Cheirocrinus* cf. *nodosus* (JAEKEL 1899).

Text-fig. 10.

cf. 1899 *Cheirocrinus nodosus* (ex parte). — JAEKEL 1899, p. 221, Pl. 10, fig. 12.

**Holotype** of *Ch. nodosus*: — RM Ec 5153, which is a gutta-percha cast taken from the specimen RM Ec 5152.<sup>6</sup>

**Type locality:** — Hedenstad, Norway.<sup>7</sup>

**Type stratum:** — Black clay-shale, Ogygiocaris shale [Lower Llandeilian], according to the label accompanying the sample.

**Material:** — Two isolated plates, neither of them complete, were thought to be designated properly as *Cheirocrinus* cf. *nodosus*.

**Remarks and discussion:** — A prominent feature of the specimens in hand is the strong sculpture of the umbo and one axial ridge,

<sup>6</sup> In the explanation of his Pl. 10, fig. 12, JAEKEL 1899 erroneously gave SGU as depository of the holotype.

<sup>7</sup> In the explanation of his Pl. 10, fig. 12, JAEKEL 1899 erroneously stated the type locality to lie in Sweden.

these being provided with protuberances similar to those figured by JAEKEL for *Ch. nodosus* but smaller and not so richly differentiated (text-fig. 10). This is the reason why the writer has not proposed an unreserved identification. Our specimens are also considerably smaller than JAEKEL's holotype, which, however, is almost flat, whereas in our material the umbo is well elevated.

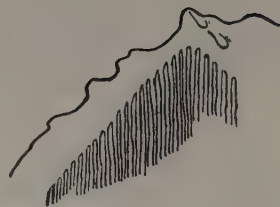
JAEKEL (1899, p. 221) referred to *Cheirocrinus nodosus* two Norwegian specimens figured by ANGELIN (1878 a, Pl. 12, figs. 16—17) as *Glyptocystites Leuchtenbergi*. One of these seems to have got lost.

The other one [RM Ec 5167, Hovindsholm] — ANGELIN's figs. 16, 16 a on Pl. 12 — which shows a fragmentary plate in internal view, cannot possibly belong to *Cheirocrinus nodosus* but should, according to the opinion of the present author, rather be referred to *Cheirocrinus granulatus* (JAEKEL). The impressions on the inside of the test, visible in ANGELIN's fig. 16 a, indicate that the plates are finely granulated, and the pectinirhombs are of the same type as in the species mentioned (cf. JAEKEL 1899, Pl. 11, fig. 4). It may be worth mentioning that HOLTEDAHL (1909, p. 9) listed a fragment from stage 4 a  $\beta$  at Hovindsholm as *Cheirocrinus penniger* EICHWALD, with a mark of interrogation though. The same species was mentioned from that locality already by KJERULF (1865, p. 4). BRÖGGER (1882, p. 42, foot-note 1) remarked that this form "sich kaum sicher bestimmen lässt". Now *Cheirocrinus penniger*, as conceived by F. SCHMIDT 1874, comprised *Ch. granulatus* too.

The specimen figured by ANGELIN, Pl. 12, figs. 17, 17 a, 17 b, might be congeneric with that of fig. 16, but can possibly have been in possession of protuberances on the axial ridges, judging from the figures. Anyhow the test was granulated. In RM there are a few more specimens from Hovindsholm, which do not supply further information, however.

**Regional distribution of *Cheirocrinus* cf. *nodosus*:** — Sweden, Västergötland: Mösseberg, Ulunda (Billingen).

**Stratigraphic range:** — The specimen from Mösseberg [RM Ec 3292] is enclosed in a grey crystalline limestone, undoubtedly of the age of the Lower Asaphus zone. The rock of the Ulunda specimen [RM Ec 2767] is a dense, lighter grey limestone, indicating a higher stratigraphic position, probably the zone of *Iliaenus schroeteri* ("*I. chiron*"), which is the youngest member of the Asaphus series in Sweden. The sample is strongly weathered and may represent a boulder.



Text-fig. 10. *Cheirocrinus* cf. *nodosus* (JAEKEL) [RM Ec 2767]. Profile view of an isolated thecal plate.

× 3.— Västergötland:  
Ulunda.



### *Cheirocrinus* sp.

Under this heading are included six more or less fragmentary plates from the Chasmops series of Västergötland, four of them from Ljungstorp, one from Mösseberg, one from a locality not closely known [all in RM]. They occur in a dark splintery lime-free or slightly calcareous rock, and all specimens are preserved as moulds. They seem to be referable to one and the same species. Possibly conspecific with them is a fragment of a *Cheirocrinus* from the Lower Chasmops limestone at Böda Harbour, Öland [RM Ec 4421].

The fossil material in question is too poor to be determined specifically. There is, however, a rather considerable resemblance to certain Norwegian forms referred to above in discussing *Cheirocrinus* cf. *nodosus*. These specimens were tentatively designated as *Cheirocrinus granulatus* (JAEKEL). And it is not unlikely that our specimens also belong to the *penniger-granulatus*-complex. According to JAEKEL (1899, p. 220), *Cheirocrinus granulatus* differs from *Cheirocrinus penniger* in being twice as large and in having the thecal plates densely granulated between the axial ridges. The last-mentioned character is not visible in our specimens. Yet this can be due to the unsatisfactory state of preservation. In size — one plate [RM Ec 3166] measures about 30 mm in long diameter — the Swedish specimens tend to *Cheirocrinus granulatus* rather than to *Cheirocrinus penniger*. The former species appears in the East Baltic provinces in the Kukruse stage ( $C_2$ ), which is equivalent to the Lower Chasmops limestone of Sweden, whereas *Cheirocrinus penniger* belongs to a somewhat lower horizon, viz.  $B_3-C_1$  (SCUPIN 1928, p. 172).

### Family **Echinoencrinitidae** (BATHER) BASSLER 1938.<sup>8</sup>

To the genera *Echinoencrinites* MEYER and *Prunocystites* FORBES known from of old, JAEKEL (1895) added *Schizocystis* and (1899) *Erinocystis*, *Glaphyrocystis*, and *Scoliocystis* to be included in the family Scoliocystidae. Later (JAEKEL 1918, p. 96) *Schizocystis* was placed in the family Callicystitidae. Its position is disputable, however, and JAEKEL's arrangement of 1918 was not accepted by e.g. ZITTEL-BROILI (1924, p. 217) and BASSLER (1938, p. 11). For reasons set forth by BATHER (1913, p. 429, § 272), the name Scoliocystidae had to be dropped for Echinoencrinidae, changed later into Echinoencrinitidae.

The genus *Eutretocystis* was established by PHLEGER in 1935 (p. 200).

<sup>8</sup> BASSLER 1938 (p. 11) referred to PHLEGER as emendator of the family-name. As far as the present writer is aware this is not correct. PHLEGER 1935 (p. 194) used the term "Echinoencrinidae BATHER", and this might have been the only instance in which he dwelled upon the subject.

It was said to be "like *Echinoencrinites* in all respects except in the development of an extra pectinirhomb on plates 10 [L 3] and 15 [R 3]". Whether the mentioned character is so important as to be constitutive of a separate genus seems to be somewhat doubtful.

For the reception of certain divergent forms the present writer could not avoid to establish a new genus, *Proctocystis*.

### Genus *Echinoencrinites* MEYER 1826.

**Genotype:** — *Echinoencrinites senckenbergii* MEYER 1826.

**Synonyms:** — See BASSLER 1938 (p. 90). The following additions may be made: — *Echinosphaerites* (ex parte) SCHLOTHEIM 1826; PANDER 1830. — *Gonocrinites* (ex parte) LEUCHTENBERG 1843. — [Non: *Echino-encrinus* (*Echino-encrinites*) FORBES 1848.<sup>9</sup> — *Echinoencrinites* BARRANDE in museo.<sup>10</sup>]

**Regional distribution:** — USSR, Estonia, Sweden, Norway,<sup>11</sup> Burma.<sup>12</sup>

**Stratigraphic range:** — Middle Ordovician.

On account of the rich variation of certain forms contained in this genus, some difficulties are involved in the dividing into species of the form-complex concerned. The taxonomic units recognized by JAEKEL (1899, pp. 247—249) were criticized by LAMANSKY (1905, p. 178), who pointed out that JAEKEL's system on the one hand goes too much into details in certain respects but on the other hand does not pay attention to several mutations, which it would have been equally justified to regard as distinct species. PHLEGER (1935, p. 196) emphasized for *Echinoencrinites senckenbergii* that the "apparent variation in ornamentation, caused by the increase in total number of folds [on the thecal plates], is a direct function of size, and although apparently marked between large and small specimens, in the opinion of the writer does not indicate specific differences".

The present writer can give no contributions to the taxonomy of the genus from the very limited East Baltic material available and the still smaller Swedish material.

For a long time *Echinoencrinites* was not known to occur outside USSR and Estonia, as was stated expressly by EICHWALD (1845, p. 104) and VERNEUIL (1845, p. 29). Yet the last-mentioned author remarked that the genus would be represented in Gotland and Britain also, if it could be trusted that *Cornulites* should be interpreted as the stem of *Echinoencrini-*

<sup>9</sup> Referred by JAEKEL to *Prunocystites* and *Schizocystis*.

<sup>10</sup> Cf. JAHN 1893, p. 399, foot-note 2.

<sup>11</sup> BRÖGGER, 1882, p. 42.

<sup>12</sup> Reported from Burma by REED 1906 (p. 25), 1917 (p. 19), 1936 (p. 11).

tes.<sup>13</sup> The first find of a specimen of *Echinoencrinites* in Sweden was announced by JAEKEL (1899, pp. 149, 248). This unique specimen of *Echinoencrinites senckenbergii* is the only representative of its genus reported in literature up till now. It is true that ANGELIN (1878 a, Pl. 12, figs. 6—12) figured specimens of "*Echinoëncrinus Senckenbergi*" (as was proposed, cf. below), but the specimens in question were derived from USSR. They were not mentioned in the text.

*Echinoencrinites* cf. *reticulatus* JAEKEL 1899.

Pl. 2, figs. 15—16.

- cf. 1830 *Echinosphaerites angulosa* (ex parte). — PANDER, p. 146, Pl. 2, figs. 28—29.  
 cf. 1842 *Echino-Encrinus striatus*. — VOLBORTH, column 303, Pl. 1, figs. 5, 11—12; Pl. 2, fig. 1.  
 1878 *Echinoëncrinus Senckenbergi* H. v. MEYER (ex parte). — ANGELIN 1878 a, Pl. 12, figs. 9—11.<sup>14</sup> (Pl. 13, figs. 1—3?).  
 cf. 1899 *Echinoencrinites reticulatus*. — JAEKEL, p. 248, Pl. 10, fig. 15.  
 cf. 1905 *Echinoencrinites reticulatus* PAND. [sic!]. — LAMANSKY, pp. 79, 178.  
 cf. 1911 *Echinoencrinites reticulatus* JAEKEL. — BASSLER, p. 20.  
 cf. 1928 *Echinoencrinites reticulatus* PAND. [sic!]. — SCUPIN, p. 171.

**H o l o t y p e** of *E. reticulatus*: — The specimen figured by JAEKEL 1899, Pl. 10, fig. 15. **F o r m e r d e p o s i t o r y**: — The then Imp. Academy of Sciences of St Petersburg.

**T y p e l o c a l i t y**: — Leningrad, USSR.

**T y p e s t r a t u m**: — So-called Vaginatum limestone, B<sub>3</sub>—C<sub>1α</sub>, Middle Ordovician.

**M a t e r i a l**: — To this species were referred 5 specimens, one of which is very well preserved [RM Ec 3353], the others being more or less imperfect. One of the two Russian specimens in the ANGELIN collection (cf. the list of synonyms above) was thought to be conspecific with the Swedish form.

**D e s c r i p t i o n**: — **G e n e r a l s h a p e** of the theca. When seen in lateral view the theca is roughly rounded or polygonal in outline. The

<sup>13</sup> The peculiar opinion of *Cornulites* as the stem of *Echinoencrinites* was set forth originally by VOLBORTH (1842). Even two years earlier *Cornulites* was brought in connexion with "les Crinoidées à tiges" by EICHWALD (1840, p. 189). Later that author was inclined to refer "die grossen Cornuliten" to *Cheirocrinites* (EICHWALD 1856, p. 123). The proposal was rejected altogether by FORBES (1848, p. 493). Further objections were raised by SALTER in "Appendix A" (1852, p. i) to MCCOY 1851. Still in 1852 HALL (p. 235) emphasized the similarity between *Cornulites* and stems of cystoids. — It needs hardly to be said that the proposed identification depends on a superficial resemblance, and that it is made impossible already by the fact that *Echinoencrinites* and *Cornulites* have quite different stratigraphic appearance.

<sup>14</sup> ANGELIN's fig. 12 on Pl. 12, showing brachioles of *Echinoencrinites*, is copied from VOLBORTH 1845, Pl. 3, fig. 1; this fig. might represent *E. angulosus* (PANDER).



base-surface is flattened. The tapering of the theca in oral direction is inconsiderable, as well as the projection of the periproctal area. The theca is pronouncedly compressed from the sides.

| (Measurements in mm)                             | RM Ec 3353 | RM Ec 3354 | RM Ec 3355 |
|--------------------------------------------------|------------|------------|------------|
| Height of the theca .....                        | 13         | 12.5       | 9.3        |
| Greatest diam. in the anal plane .....           | 12.4       | 12.3       | 9.3        |
| Greatest diam. transverse to the anal plane .... | 9.1        | 10.5       | 8          |

As far as sutures between the thecal plates are discernible they indicate a construction of the thecal skeleton according to the general plan in *Echinoencrinites*, which agrees largely with the diagram communicated in text-fig. 5.

**Surface structures of stereom.** The thecal plates are ornamented with axial ridges extending from a slightly elevated umbonal region. Owing to branching the number of radiating folds increases from about 10 in the centre to about 20—25 at the periphery of the plate (on *LL* and *ILL*). Besides the radial elements there is a system of faint concentric folds, forming transverse ridges between the axial folds. The number of transverse ridges between two radial ridges extending from one umbo to another amounts to about 20.

**Pores of the thecal plates.** Two basal disjunct pectinirhombes are present, located in *IL* 1—*B* 2 and *B* 2—*IL* 2. The upper rhomb is situated in *R* 3—*L* 4. The specimen RM Ec 3353 displays an additional demi-rhomb in *R* 1.

**The ambulacral area** is rectangular and has five reniform brachiole-facets. Gonopore and hydropore are not recognizable in any specimen available.

**Alimentary canal.** The mouth is subcircular, lying in the centre of the ambulacral area. The anus is surrounded by *IL* 4, *L* 5, and *IL* 5, which are swelled up forming a triangular field around the rim of the large anal opening.

**The base-surface** is flattened with a large quadrangular invagination in which the stem is inserted. Only in one specimen [RM Ec 3355] a few proximal columnals are preserved. They are circular with a wide lumen.

**Discussion:** — The Swedish form now dealt with is evidently closely allied to *Echinoencrinites reticulatus* JAEKEL. It differs chiefly by its smaller size and by the smaller number of axial ridges on the thecal plates. According to JAEKEL (1899, p. 248) the height of the mentioned species is about 25 mm and the width about 20 mm. The number of axial ridges on *ILL* was given at 40. In comparison with this our largest specimens attain

only half the size and have only about half the number of axial folds. If we call to mind what was said above in the introductory remarks on *Echinoencrinites*, we may perhaps be inclined to consider the mentioned differences insignificant, on account of which the Swedish form might be identified with *Echinoencrinites reticulatus* without any reserve. In recognition of the obscure points in the taxonomy of the genus, the present author yet thought it preferable to use the open nomenclature.

The specimen RM Ec 5513 (USSR, locality not indicated) figured by ANGELIN (1878 a, Pl. 12, figs. 9—11) may safely be regarded as conspecific with the Swedish form. For it agrees in shape of the theca, size, and ornament of the thecal plates. ANGELIN's figures are rather unsatisfactory, however, as might appear from a look at our Pl. 2, fig. 15, in which the specimen is orientated in the same way as in ANGELIN's Pl. 12, fig. 10.

It should also be noted that the specimen figured by VOLBORTH (1842, Pl. 1, figs. 11—12) with regard to shape comes very close to the form here described, differing only in size and in number of axial folds on the thecal plates. The specimen was referred by VOLBORTH to *Echinoencrinites striatus* (PANDER), a determination which cannot be confirmed, however. Furthermore it seems to be a typical representative of *Echinoencrinites reticulatus*.

Whether "*Echinoëncrinus* n. sp." listed by LINDSTRÖM (1888 a, p. 10) from the "Lower gray Orthoceratite Limestone" refers to this species or to *Proctocystis monstrosa* n. sp. cannot be decided.

**Regional distribution of *Echinoencrinites* cf. *reticulatus*:** — Sweden, Östergötland: Vadstena,<sup>15</sup> Kungs Norrby, Västanaå. — USSR (probably the Leningrad district only).

**Stratigraphic range:** — The Swedish specimens originate undoubtedly from the Expansus (Lower Asaphus) limestone in the middle of the Asaphus series, Upper Arenigian, equivalent to the so-called Vaginatum limestone of the East Baltic area.

### *Echinoencrinites senckenbergii* MEYER 1826.

Pl. 2, fig. 17. Pl. 3, fig. 1. Text-fig. 11.

- 1826 *Echino-Encrinites Senckenbergii*. — MEYER 1826 a, p. 185, Pl. 2, figs. 1—5.  
 1826 *Echinospaerites Granatum*. — SCHLOTHEIM, column 311, Pl. 1, figs. 1 a—c [fig. 1 a inverted].  
 1826 *Echino-Encrinites Senckenbergii*. — MEYER 1826 b, p. 232.

<sup>15</sup> On the geologic map-sheet Vadstena (Sver. Geol. Unders. Ser. Aa. 130. Stockholm, 1906) a quarry in Orthoceratite limestone is marked about 1 km S of Vadstena. This is the only exposure in the immediate neighbourhood of the town. It might be probable, therefore, that our specimens were collected at the said locality.

- 1852—54 *Echinoencrinus Senckenbergii* (ex parte). — ROEMER, p. 272, Pl. 4, figs. 1 a—c [cop. from MEYER 1826 a].  
 1899 *Echinoencrinites Senckenbergii* H. v. MEYER 1826. — JAEKEL, p. 248, Pl. 13, figs. 1—3.  
 1905 *Echinoencrinites Senckenbergi* H. v. MÜLLER [sic!]. — LAMANSKY, pp. 79, 178.  
 1911 *Echinoencrinites senckenbergi* MÜLLER [sic!]. — BASSLER, p. 20.  
 1935 *Echinoencrinites senckenbergii* VON MEYER. — PHLEGER, p. 195, Pl.-figs. 4—8.

**Holotype:** — The specimen figured by MEYER 1826 a, Pl. 2, figs. 1—5. According to BUCH (1846 a, p. 109) the type-specimen has been lost.

**Type locality:** — Not known (USSR or Estonia).

**Type stratum:** — Not known [it may be inferred that MEYER's specimen originated from some layer of stage B<sub>3</sub> (Middle Ordovician), from where the East Baltic material of this species is generally reported].

**Material:** — The hypotypoid published by JAEKEL (1899, Pl. 13, fig. 3) [RM Ec 3370], which is a fairly well preserved theca with attached proximal portion of the stem (the stem-fragment was not represented in JAEKEL's figure); the actinal region of the theca is wanting. It seems to have been ground down, probably by JAEKEL. Further there is an isolated incomplete stem [RM Ec 3371].

**Description:** — General shape of the theca. The specimen, which is a little deformed, has roughly the shape of a globular body but is clearly tapering towards the upper pole (text-fig. 11; in Pl. 2, fig. 17, and in Pl. 3, fig. 1, the theca is observed somewhat from below on account of which the tapering portion is not visible).

**Measurements.** Height of the theca 29.5 mm. Diameter at the widest portion of the theca 26.5 mm.

The construction of the thecal skeleton is according to the regular type of *Echinoencrinites*.

**Surface structures of stereom.** A frame of low and relatively broad ridges gives a reticulate appearance to the surface of the plates. In a well-preserved plate (IL 3) in our specimen the number of radiating ridges is about 15 at the centre. By dividing, this number is increased to 60 in the periphery of the plate. The number of transverse elements between two axial folds extending from umbo to umbo of two adjacent plates is 24—28, which means 4—5 in 2 mm. A special structure is developed on the plates bordering the anus, viz. a narrow triangular eminence, the vertex of which lies in the plate-centre and the base at the edge of the anus. In this way the anus becomes enclosed in a triangular area with its vertex directed upwards. — The umbo of certain plates is rather projecting, but on the whole most plates are tolerably flattened.

**Pores of the thecal plates.** Disjunct pectinirhombs are developed in IL 1—B 2 and B 2—IL 2. On the two ILL the pores do not by



far stand out as clearly as marked in JAEKEL's figure (1899, Pl. 13, fig. 3). Nor was the writer able to confirm the presence of demi-rhombs on  $B1-B2$  and  $B2-B3$  indicated by JAEKEL. Yet it could be stated in a Russian specimen [RM Ec 5523] that such demi-rhombs occur in *Echinoencrinites senckenbergii*. — The upper rhomb, on  $R3-L4$ , is only partially discernible.

The ambulacral area is unfortunately lacking in the Swedish specimen, as mentioned above. In the Russian specimen just referred to, it is ovate, being surrounded by a slightly raised edge. It has 10 (or 11?) brachiole-facets. Five faint and short ambulacra radiate from the mouth. Each ambulacrum, branching dichotomously, connected two brachioles with the mouth. — The gonopore is located in a stereomic swelling and is bisected by the suture between  $O5$  and  $O1$ . The gonopore is also visible on the ground top-surface of RM Ec 3370, as well as a dumb-bell-shaped hydropore (cf. figs. 24—25 of JAEKEL 1899, Pl. 13; a good figure of the actinal region in *Echinoencrinites* was given by JAKOVLEV 1927, fig. 1, p. 55, in which the designations of gonopore and hydropore have to be changed, however, as observed by JAKOVLEV 1930, p. 31).

**Alimentary canal.** The mouth is in the same Russian specimen a small ovate slit extended in the direction of the ambulacral area. The gut opens — as usual in *Echinoencrinites* — in interradius IV—V. The anus, which is crushed in our unique Swedish specimen but otherwise large and circular, is thus situated between  $IL4$ ,  $L5$ , and  $IL5$ . The development of the surrounding skeleton tissue was already described above.

The base-surface is somewhat flattened and is provided with a large quadrangular invagination (length of side 8 mm), from where the stem emerges at an oblique angle to the vertical axis of the theca. This position of the stem caused JAEKEL (1918, p. 95) to propose the theca to have been resting with the base-surface directly on the sea-floor, the stem having lost its function of supporting the theca. — Some 10 columnals are still attached to the theca in our specimen. They are compressed secondarily. The isolated stem-fragment [RM Ec 3371] is conical in shape and consists — at a length of 13 mm — of 14 circular and wide-lumened columnals. To judge from the construction of the stem it must have been contractile. Therefore, if resting freely on the substratum, the animal seems to have been capable of a certain change of position.

**Discussion:** — It is possible that the species *Echinoencrinites senckenbergii* is composed of a few subspecies or varieties, differing from



Text-fig. 11. *Echinoencrinites senckenbergii* MEYER [RM Ec 3370]. Sketch of outline of the theca in posterior view. Nat. size. — Östergötland: Kungs Norrby.

each other mainly in regard to the shape of the theca. The figures of the holotype communicated by MEYER (1826 a, Pl. 2, figs. 4—5) show an almost pentagonal theca tapering strongly upwards from the widest portion, which is to be found — reckoned from the base — in a plane at one third of the total height of the theca. The specimen figured by JAEKEL (1899, Pl. 13, figs. 1—2) is decidedly more rounded in outline, though clearly tapering in oral direction. It is somewhat higher than wide, which is also true of MEYER's specimen. Measured in his fig. 4, the difference between height and width is inconsiderable, however. PHLEGER (1935, p. 198) thought it convenient to erect a new species, *Echinoencrinites spheroidalis*, for a form with spherical theca. Its relations were explained as follows: — "This species is most closely related to *Echinoencrinites senckenbergii* VON MEYER, but it differs in being as wide as high, in having more radial folds per unit size, in having the anus less projected from the theca, in having narrow, smooth eminences extending from the anus to the beaks of the enclosing plates, and in the comparative flatness of the plate beaks" (PHLEGER 1935, p. 199). As far as the present author is aware, the given characters — irrespective of the spherical shape of the theca — are not specific to the form in question. The number of radial folds on each plate was stated by PHLEGER to be 40—50. In MEYER's fig. 2, which shows an enlarged plate from the holotype, at least 70 radial folds are to be counted. JAEKEL (1899, p. 249) gave the highest number at 90. In our specimen there are 60, as we have seen. On a preceding page of his paper PHLEGER pointed out, moreover, that variations in number of axial ridges do not indicate specific differences (cf. p. 78 above). Nor have small variations in the degree of projection of anus and umbos specific importance. For these reasons the species proposed by PHLEGER might not have higher taxonomic rank than that of a subspecies or variety.

In comparing the Swedish specimen with the Russian material available to him, JAEKEL (1899, p. 248) remarked that the tapering of the theca is more pronounced in the latter. On that account our form would approach to *Echinoencrinites senckenbergii spheroidalis* PHLEGER. Yet on the whole it seems to agree more with the typical form as described by JAEKEL and, therefore, might properly be referred to the nominate form.

Regional distribution: — Sweden, Östergötland: Kungs Norrby. — Estonia. — USSR (probably the Leningrad district only). — ? Burma.<sup>16</sup>

<sup>16</sup> REED (1906, p. 26) reported *Echinoencrinites* cf. *senckenbergii* from the northern Shan States. — JAEKEL (1899, p. 248) listed the species from Norway, though with a mark of interrogation. This statement is undoubtedly based on BRÖGGER's notes on the genus (1882, p. 42). But BRÖGGER included several species under the name of "*Echinoencrinus Senckenbergii*" and stated that the sparse Norwegian specimens seem to agree best with *Echinoencrinites angulosus* (PANDER).

**Stratigraphic range:** — The Swedish specimens were collected from the *Expansus* (Lower *Asaphus*) limestone, the East Baltic material is from the stage B 3 (*Vaginatum* limestone), i.e. strata of Upper Arenigian age.

Genus *Proctocystis* n.

**Genotype:** — *Proctocystis monstrosa* n. sp.

**Synonym:** — *Echinoëncrinus* (ex parte) ANGELIN 1878 a.

**Derivation of name:** — From Greek *πρωκτός*, tail, in allusion to the conspicuous periproct.

**Diagnosis:** — A genus of Echinoencrinitidae with the number of *RR* reduced to 4; *RR* not, or moderately, prolonged; *L* 3 depressed into the circlet of *ILL* so as to come in contact with *B* 3. *IL* 4, *L* 5, and *IL* 5 long, forming a protruding periproct.

**Discussion:** — In general appearance *Proctocystis* reminds of *Erinocystis* JAEKEL, owing to the strong development of the periproct in both genera. They also agree in another respect, viz. the depression of *L* 3 between *IL* 2 and *IL* 3, so that the *ILL* do not form a closed circlet. The same feature, moreover, is found also in *Glaphyrocystis compressa* JAEKEL (1899, pp. 253, 257).<sup>17</sup> An important difference from *Erinocystis* and other genera of Echinoencrinitidae is the suppression of *R* 5. The *RR* are not especially prolonged as in *Erinocystis*. — In outline *Proctocystis* displays a certain resemblance even to *Echinoencrinites striatus* (PANDER).

**Regional distribution:** — Sweden, USSR.

**Stratigraphic range:** — Middle Ordovician.

*Proctocystis monstrosa* n. sp.

Pl. 3, fig. 2. Text-figs. 12—13.

**Derivation of name:** — The specific name was chosen in view of the strange appearance of this form.

**Holotype:** — RM Ec 3350.

**Type locality:** — Vadstena, Östergötland.<sup>18</sup>

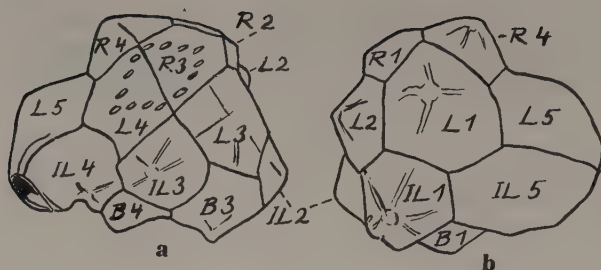
**Type stratum:** — *Expansus* (Lower *Asaphus*) limestone, middle part of the *Asaphus* series, Middle Ordovician.

**Material:** — Two specimens are available. The theca of the holotype is on the whole well preserved, but the very actinal region is wanting;

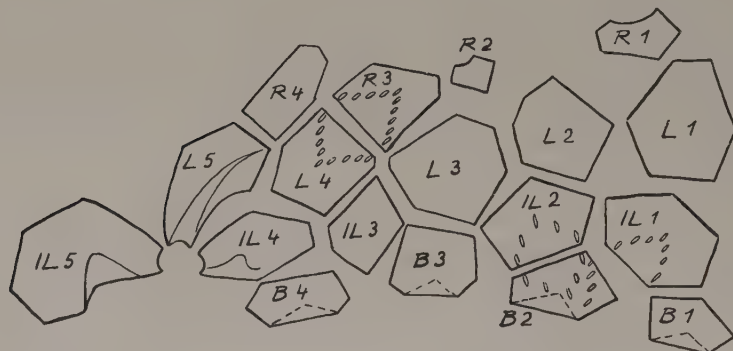
<sup>17</sup> In the other species of this genus described by JAEKEL, *Glaphyrocystis wöhrmanni*, the *ILL* form an uninterrupted circlet.

<sup>18</sup> Cf. p. 81, foot-note 15.





Text-fig. 12. *Proctocystis monstruosa* n. sp. [RM Ec 3350], holotype. a Right lateral view. b Left lateral view.  $\times 2$ . — Östergötland: Vadstena.



Text-fig. 13. *Proctocystis monstruosa* n. sp. Analysis of the theca in the holotype [RM Ec 3350].

a few columnals are attached to the base. The second specimen [RM Ec 3351] is more imperfect.

**Diagnosis:** — A species of *Proctocystis* in which the *RR* are not prolonged; several plates with high umbo and 4—5 axial ridges considerably stronger than the main part of the ornament; periproct strongly protruding.

**Description of the holotype:** — General shape of the theca. Irrespective of the periproct and the salient apices of most plates, the theca has roughly the shape of a globular body. With all its projecting angles it has the appearance of a so-called “morning star”.

**Measurements.** Height 12.5 mm; length (measured over the periproct) 17 mm; width (measured at right angles to the length) 12 mm.

**Thecal skeleton.** The peculiarities in the construction of the theca were mentioned already in the diagnosis and are further elucidated in text-fig. 13, which also gives an idea of the shape of the single plates. Of the plates forming the periproct especially *IL 5* is distorted. Below the anus this plate has a trough-shaped depression widening to flow together with a similar depression on the subanal side of *IL 4*. *L 3*, which is pressed down through the *IL*-circlet to rest upon *B 3*, is remarkably flatter than the other plates, several of which are conic owing to the high umbos. The four *RR*

are very different in shape and size. Two of them are small, which is true in the first place of *R* 2, whereas two are considerably large. For *R* 3 this might be due to the development of the demi-rhomb integrating in the upper pore-rhomb.

*OO* are likely to have been rudimentary as in *Erinocystis*.

**Surface structures of stereom.** As usual in the Echinoecrinidae the plate ornament is made up of two systems of folds, one radial and one concentric. The most sculptured ornament is present in the plates of the lateral cycles. In *IL* 2 there are 5 coarse ridges radiating from the high umbo. The number of weaker ridges is about 20 in the periphery of the plate. *L* 1, which is larger, has 4 main ridges and about 30 finer ones. In the centre the number of ridges is less, to increase towards the periphery by dividing. As mentioned in the diagnosis, all axial ridges are about equally dimensioned in some plates.

The faint concentric ridges form together with the radial ridge system a somewhat irregular lattice. Between two axial folds extending from umbo to umbo of two adjacent plates there are 20—25 transverse folds, which means about 7 in 2 mm.

**Pores of the thecal plates.** Two basal pore-rhombs are present, on *IL* 1—*B* 2 and *B* 2—*IL* 2. Only a few pore-slits are visible. The upper rhomb lies on *R* 3—*L* 4.

The ambulacral area is unfortunately not preserved. So nothing can be stated of the number of brachioles, nor of hydropore and gonopore. As a matter of course the mouth is not preserved. The anus is a rounded opening (diam. about 3 mm) directed downwards. The periproct is formed by *IL* 4, *L* 5, and *IL* 5.

**The base surface.** *BB* are invaginated so as to form a quadrangular depression (length of sides about 5.5 mm), in which the stem is inserted. The fragmentary columnals attached to the thecal base are oval in outline. The long diameter is 4.4 mm and the short one 3.5 mm. It has a wide lumen.

**Remarks on the second specimen available:** — This specimen [RM Ec 3351] is more worn than the holotype and considerably more damaged. It shows, however, most of the characters described of *Proctocystis monstrosa*, on account of which it was referred to that species. Yet it should be remarked that the periproct is less prominent than in the holotype. In this respect it approaches to *Proctocystis rossica* n. sp. (cf. below).

**Discussion:** — It was pointed out above (p. 85) that *Proctocystis* agrees in certain respects with *Erinocystis*. And species of that genus have some resemblance in habit to *Proctocystis monstrosa* (see e.g. JAEKEL 1899, Pl. 13, figs. 6—6 a). JAEKEL (1899, p. 251) observed that members of *Erinocystis* are characterized by an intense brownish yellow colour. The speci-

mens being free from the rock, he was not able to decide, however, whether this colour is a primary feature or caused by the matrix in which the specimens had been embedded. It may be worth mentioning that the holotype also of the species here discussed has a yellow colour, which is, indeed, rarely met with elsewhere in our material. The second specimen of *Proctocystis monstrosa*, on the other hand, is rather greyish white. — The differences from *Erinocystis* were demonstrated above.

In describing *Echinoencrinites striatus* (PANDER), JAEKEL (1899, p. 248) remarked that the periproct projects in certain specimens almost as much as in *Erinocystis*, which, moreover, was looked upon as an offshoot from the species mentioned. It is obvious that such specimens of *Echinoencrinites striatus* may be rather similar to *Proctocystis monstrosa*, as is visible from the figures delivered by VERNEUIL (1845, Pl. 1, figs. 5 a—b). Otherwise the differences are great enough in construction and ornament of the theca.

To *Proctocystis* we have to refer one more species, represented by the specimen figured rudely by ANGELIN (1878 a) on Pl. 12, figs. 6—8, under the name of *Echinoëncrinus Senckenbergi* H. v. MEYER. For this Russian species, which seems to be closely related to the Swedish form, the name *Proctocystis rossica* is proposed.<sup>19</sup>

Regional distribution: — Sweden, Östergötland: Vadstena.

Stratigraphic range: — As in the case of *Echinoencrinites* cf. *reticulatus* we have to assume that *Proctocystis monstrosa* originates from the Expansus (Lower Asaphus) limestone, Upper Arenigian.

## Family Callocystitidae (BERNARD) BASSLER 1938.

### Subfamily Apiocystinae JAEKEL 1899.

An elucidatory survey of the contents of the subfamily was given in 1904 by SCHUCHERT. Before then JAEKEL (1899) had contributed to the knowledge of the forms concerned. He described as *Meekocystis* an Ordo-

<sup>19</sup> *Proctocystis rossica* n. sp. (Pl. 3, fig. 3). Synonym: — *Echinoëncrinus Senckenbergi* H. v. MEYER (ex parte). — ANGELIN 1878 a, Pl. 12, figs. 6—8. Holotype: — RM Ec 5509. Type locality: — An unknown locality (in the Leningrad district?), USSR. Type stratum: — Unknown. Material: — One specimen, the holotype. Diagnosis: — A species of *Proctocystis* in which the RR are somewhat prolonged; most plates flattened or moderately conic; no strong ridges in the radial ornament system; periproct projecting moderately. Measurements: — Height 16 mm; length (measured over the periproct) 19 mm; width (measured at right angles to the length) 16 mm. Pores: — As in *P. monstrosa*. Remarks: — In comparison with the Swedish species the present form is more tapering upwards, and periproct and umbos do not project as much.



vician species from N. America, for which yet CARPENTER (1891, p. 10) had proposed the name *Lepadocystis*. This genus was discussed closely by FOERSTE (1914, p. 458 seq.), who showed i.a. that 5 pectinirrhombs are present. A second species was announced by PARKS (1910). Further JAEKEL erected the genus *Hallicystis*. *Apiocystites* FORBES 1848 and *Lepocrinites* CONRAD 1840 were not held apart and were wrongly referred to under the first-mentioned name along with our new genus *Lovénicystis* and some N. American species. Of these "*Apiocystites*" *canadensis* BILLINGS was transferred by SCHUCHERT (1904, p. 211) to *Callocystites*, whereas "*Apiocystites*" *huronensis* BILLINGS and "*A.*" *tecumsethi* BILLINGS were later recognized as members of a separate genus, *Brockocystis* FOERSTE, of which a few other species have been described (FOERSTE 1914, 1919).

BATHER (1900, p. 61; 1913, p. 433, § 281) took *Apiocystites* as a synonym of *Lepocrinites* ("*Lepadocrinus*") and was in doubt of the validity of *Hallicystis* JAEKEL. This genus is well established, however.

Some new genera, *Jaekelocystis* SCHUCHERT 1903 and *Tetracystis* SCHUCHERT 1904, were erected for species of the rich fauna of Callocystitidae in the Silurian and Devonian deposits of N. America. EHLERS & LEIGHLY (1922, p. 155), finally, presented an interesting Middle Devonian genus, *Lipsanocystis*, which is the youngest known representative of the Apio-cystinae.

To these genera we have to add *Lovénicystis* n. g.

The morphological differentiation within the subfamily may be demonstrated to some extent in the following table: —

- |         |                                                                                                                                                     |                                        |
|---------|-----------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------|
| 1 (4).  | 5 ambulacra; more than 3 pectinirrhombs; <i>LL</i> and <i>RR</i> in closed circlets; anus between <i>IL</i> 4— <i>IL</i> 5— <i>L</i> 4— <i>L</i> 5. |                                        |
| 2 (3).  | 5 pectinirrhombs; <i>IL</i> 4 and <i>IL</i> 5 elongated vertically .....                                                                            | <i>Lepadocystis</i> CARPENTER.         |
| 3 (2).  | 4 pectinirrhombs; <i>IL</i> 4 and <i>IL</i> 5 not elongated                                                                                         | <i>Brockocystis</i> FOERSTE.           |
| 4 (1).  | 4 ambulacra; 3 pectinirrhombs.                                                                                                                      |                                        |
| 5 (12). | <i>LL</i> and <i>RR</i> in closed circlets.                                                                                                         |                                        |
| 6 (7).  | Anus enclosed by 4 plates ( <i>IL</i> 4— <i>IL</i> 5— <i>L</i> 4— <i>L</i> 5); <i>IL</i> 4 and <i>IL</i> 5 elongated .....                          | <i>Lovénicystis</i> n. g.              |
| 7 (6).  | Anus enclosed by less than 4 plates.                                                                                                                |                                        |
| 8 (11). | Anus enclosed by 3 plates ( <i>IL</i> 4— <i>IL</i> 5— <i>L</i> 5); <i>IL</i> 4 and <i>IL</i> 5 not elongated.                                       |                                        |
| 9 (10). | Pectinirrhombs short, with few pores; ambulacra continuing nearly or right down to the stem .....                                                   | <i>Apiocystites</i> FORBES.            |
| 10 (9). | Pectinirrhombs long, angulated, with numerous pores; ambulacra usually not longer than one-half the height of the theca .....                       | <i>Lepocrinites</i> CONRAD.            |
| 11 (8). | Anus enclosed mainly by 1 plate ( <i>L</i> 5) .....                                                                                                 | <i>Lipsanocystis</i> EHLERS & LEIGHLY. |

- 12 (5). *L*- and *R*-circlets partly interlocking; *IL* 4 and *IL* 5 more or less elongated.
- 13 (16). Anus enclosed by 4 plates (*IL* 4—*IL* 5—*L* 4—*L* 5).
- 14 (15). Pectinirhombs long, with numerous pores; anus with a marginal ring of small plates ..... *Tetracystis* SCHUCHERT.
- 15 (14). Pectinirhombs very small; anus without a marginal ring of small plates ..... *Jaekelocystis* SCHUCHERT.
- 16 (13). Anus enclosed by 3 plates (*IL* 4—*IL* 5—*L* 5); pectinirhombs with few pores ..... *Hallicystis* JAEKEL.

In the analytical table are not mentioned characters such as size, shape, and ornament of the theca, construction of the stem, &c., which may of course also be of distinctive importance.

### Genus *Lovénicystis* n. g.

Genotype: — *Apiocystites angelini* (JAEKEL 1899).

Synonyms: — *Lepadocrinus* ANGELIN 1878; LINDSTRÖM 1888; HAECKEL 1896 (ex parte). — *Apiocystites* (ex parte) JAEKEL 1899; SPRINGER 1913; ZITTEL-BROILI 1924. — *Lepocrinites* (ex parte) SCHUCHERT 1904.

Derivation of name: — The genus is named after S. LOVÉN (1809—95).

Diagnosis: — A genus of *Apiocystinae* with oval—globular theca, which is circular or slightly angular in transverse section; *LL* and *RR* in closed circlets; *IL* 4 and *IL* 5 elongated; 1 basal and 2 upper pectinirhombs, long and angulated in the adult, with fairly numerous pores; 4 ambulacra, at least some of them usually extending nearly to the base in the adult; brachioles moderately abundant; anus enclosed by 4 plates, viz. *IL* 4—*IL* 5—*L* 4—*L* 5; anus with 6 valvulae, embraced by a dorso-lateral border of small plates.

Remarks: — As appears from the list of synonyms, this genus has previously been identified either with *Lepocrinites* or with *Apiocystites*. SCHUCHERT (1904, p. 214) observed that the genotype of our new genus might belong to *Lepocrinites* and not to *Apiocystites* "on account of the large adjoining pectinirhombs, with numerous dichopores, the similar structure of the ambulacra, and the more numerous dichopores". Further features separating it from *Apiocystites* are the following: — *IL* 4 and *IL* 5 elongated vertically, which is not the case in *Apiocystites*; the anus is enclosed by 4 plates instead of 3; the anus is covered by a pyramid of 6 valvulae instead of 5 (this character might be variable, however). In *Lepocrinites*, too, *IL* 4 and *IL* 5 are not elongated, and only 3 plates border the anus; the number of pores in the pectinirhombs amounts to 40 (SCHUCHERT 1904, p. 215); as a rule the ambulacra do not continue below the equatorial region of the

|                    | <i>LL</i> and <i>RR</i> in closed circlelets; anus enclosed by 1 plate.                                                                                                                                                                                                                                                           | <i>LL</i> and <i>RR</i> in closed circlelets; anus enclosed by 3 plates. | <i>LL</i> and <i>RR</i> in closed circlelets; anus enclosed by 4 plates. | <i>L</i> - and <i>R</i> -circlelets partly interlocking; anus enclosed by 4 plates. | <i>L</i> - and <i>R</i> -circlelets partly interlocking; anus enclosed by 3 plates. |
|--------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------|--------------------------------------------------------------------------|-------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------|
| <i>Middle Dev.</i> | <i>Lipsanocystis</i>                                                                                                                                                                                                                                                                                                              |                                                                          |                                                                          |                                                                                     |                                                                                     |
| <i>Lower Dev.</i>  | <div style="display: flex; justify-content: space-around; align-items: center;"> <div style="text-align: center;"> <i>Lepocrinites</i><br/> <i>Lepocrinites</i><br/> <i>Apiocystites</i> </div> <div style="text-align: center;"> <i>Lovénicystis</i> </div> <div style="text-align: center;"> <i>Jaekelocystis</i> </div> </div> |                                                                          |                                                                          |                                                                                     |                                                                                     |
| <i>Upper Sil.</i>  | <div style="display: flex; justify-content: space-around; align-items: center;"> <div style="text-align: center;"> <i>Brockocystis</i><br/> <i>Lepadocystis</i> </div> <div style="text-align: center;"> <i>Tetracystis</i> </div> <div style="text-align: center;"> <i>Hallicystis</i> </div> </div>                             |                                                                          |                                                                          |                                                                                     |                                                                                     |
| <i>Middle Sil.</i> | <div style="display: flex; justify-content: space-around; align-items: center;"> <div style="text-align: center;"> 3 pectini-<br/>rhombs;<br/>4 ambulacra </div> <div style="text-align: center;"> 4 pectini-<br/>rhombs;<br/>5 ambulacra<br/>5 pectini-<br/>rhombs;<br/>5 ambulacra </div> </div>                                |                                                                          |                                                                          |                                                                                     |                                                                                     |
| <i>Lower Sil.</i>  |                                                                                                                                                                                                                                                                                                                                   |                                                                          |                                                                          |                                                                                     |                                                                                     |
| <i>Upper Ord.</i>  |                                                                                                                                                                                                                                                                                                                                   |                                                                          |                                                                          |                                                                                     |                                                                                     |



theca; the stem is developed distally as a leech-shaped piece of closely anchylosed columnals coated by a nodose layer (SCHUCHERT 1904, p. 214). Since *Lovénicystis* cannot be identified with any other known genus of the Apiocystinae (cf. the analytical table) it is justified and necessary to look upon it as a distinct genus.

With regard to the construction of the theca — *LL* and *RR* in closed circlets, the anus being surrounded by *IL* 4—*IL* 5—*L* 4—*L* 5 — our genus agrees with *Lepadocystis* (Richmond, Upper Ordovician) and *Brockocystis* (Brassfield, Cataract, Lower Silurian). In this respect it would thus remain on a primitive stage. But otherwise — in number (3) and development of the pectinirhombs (in earlier forms these are not always completely disjunct), in number (4) and extension of the ambulacra, and in stereom structures — *Lovénicystis* decidedly appears as an advanced type.

It is evident that a differentiation of the Apiocystinae along several morphological lines took place in the beginning of the Silurian period. This may be demonstrated in the scheme on p. 91.

Regional distribution: — Sweden.

Stratigraphic range: — Upper Silurian.

*Lovénicystis angelini* (JAEKEL 1899).

Pl. 3, figs. 4—11. Text-figs. 14—16.

- 1878 *Lepadocrinus Gebhardi* CONRAD. — ANGELIN 1878 a, p. 32, Pl. 11, figs. 29—35; Pl. 19, figs. 18, 18 a—c.  
 1888 *Lepadocrinus Gebhardi* CONR. — LINDSTRÖM 1888 b, p. 20.  
 1896 *Lepadocrinus Angelini* (nomen nudum). — HAECKEL, p. 135.  
 1899 *Apiocystites Angelini* n. sp. — JAEKEL, p. 282, Pl. 14, figs. 5—7.  
 1904 *Lepocrinites*(?) *angelini* HAECKEL. — SCHUCHERT, p. 214.

Lectotype: — RM Ec 5036, the specimen upon which JAEKEL (1899) based fig. 5 on his Pl. 14. This figure is restored, however, and is not exact. Thus ambulacrum I (to the right in the figure) is in the actual specimen very short and does by no means continue to the *B*-circlet, but just crosses the suture *R* 1—*L* 2. Further, the basal pectinirhomb lies nearer to ambulacrum II. — The state of preservation of the lectotype is not perfect, since a good deal of the anal area is damaged.

Type locality: — Lau(?), Gotland.

Type stratum: — Probably some layer of the Eke group, Lower Ludlow.<sup>20</sup>

<sup>20</sup> Neither type locality, nor stratum of this species are known with certainty, most specimens being labelled "Gotland" only. According to ANGELIN (1878 a, p. 32) the species originates from Lau, as is also stated on the labels of a few specimens. LINDSTRÖM (1888 b,

**Material:** — Besides the lectotype the following specimens — all in RM — are available to the writer: — the two paratypoids of JAEKEL 1899 [RM Ec 5037, 5038]; two specimens [RM Ec 5034, 5035] being the originals av ANGELIN (1878 a), Pl. 11, figs. 30—32, and Pl. 19, figs. 18, 18 a (the original of Pl. 11, fig. 29, was not traced); some specimens figured in LOVÉN MS (cf. above, pp. 7—8); some 30 thecae in different states of preservation; further there are a number of stem-fragments, which cannot safely be referred to this species, however.

**Diagnosis:** — Coincident with that of the genus by monotypy.

**Description of the holotype:** — General shape of the theca. The theca is oval, almost circular in transverse section.

**Measurements.** Height about 14 mm; equatorial diameter 12.3 mm (in JAEKEL's fig. 5 the scale is rather  $\times 5$  than  $\times 6$  as proposed).

**Thecal skeleton.** The construction of the theca and the shape of the plates are according to the diagrams in text-figs. 14—15.

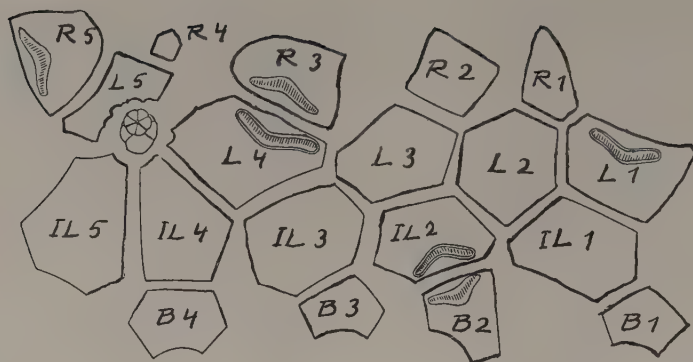
**Surface structures of stereom.** The plates are provided all over with knobs and short interlacing raised lines, forming partly a concentric ornament.

**Pores of the thecal plates.** The basal pectinirhomb is situated, as usual, in *B*2—*IL*2. Each half contains about 20 pores. Of the upper pectinirhombs that in *L*1—*R*1 has about 15 pores and that in *L*4—*R*3 about 22. The grooved recesses are angulated, with raised margins.

**Ambulacral system.** Ambulacra are present in the radii I, II, IV, and V. They are rather prominent. The ambulacrum in radius I is very short, as mentioned above, whereas the others continue to the base. Ambulacrum II is lacking for the greatest part of its length. The areas of the thecal plates upon which it has rested are smooth but show indistinct impressions of the lower sides of the plates constituting the ambulacrum. The ambulacra are constructed as illustrated in text-fig. 16: f. The parambulacralia (outer side-plates of BATHER 1900, p. 84, fig. 6) have about one-half the size of the ambulacralia (side-plates, BATHER). The last-mentioned are striated vertically on the surfaces bordering the ambulacral groove. Covering plates are not preserved in the lectotype. The location of the brachioles is also visible in our text-fig. 16: f. Since all ambulacra are more or less damaged, the number of brachiole-facets cannot be ascertained but might not have exceeded 12 along each side of the main

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p. 20) listed the species from stage "f". Dr HEDE kindly informed the author, that nothing can be inferred with certainty from the inconsiderable rock-fragments attached to the thecae, but that the nature of the matrix and the state of preservation of the fossils do not contradict the statements mentioned above. Then the specimens would originate from limestones (LINDSTRÖM's stage "f") belonging to the Eke group, and probably from reef-limestones enclosed in them.



Text-fig. 14. *Lovénicystis angelini* (JAEKEL). Analysis of the theca.

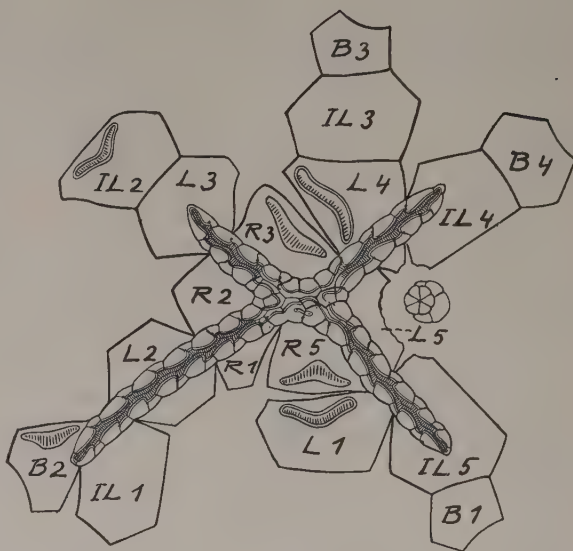
groove, from which short side-grooves run out alternately to the right and the left sides, to the small rounded or kidney-shaped brachiole-facets. The hydropore is elongated transversally but its shape is not quite clear in this specimen.

**Alimentary canal.** The mouth is a narrow slit in the centre of the ambulacral grooves. The anus, in interradius IV—V, is surrounded by 4 plates (cf. the diagnosis of the genus). No details of its structure can be made out from the specimen under discussion.

The round gonopore opens just below the hydropore.

Of the stem one proximal columnal only is present. The diameter is fully 5 mm, and the diameter of the lumen 3 mm.

**Observations on the typoids:**—In some instances the theca is more globular. A certain shape seems hardly to be confined to a distinct group of age, for more globular as well as more elongate forms are met with in both small and medium-sized specimens. The few large specimens in hand are oval, however.



Text-fig. 15. *Lovénicystis angelini* (JAEKEL). Theca projected from the oral pole. (From LOVÉN MS, Pl. 6. Modified in the ventro-anal region; symbols denoted by the present writer. About  $\frac{2}{3}$  of original size).



Measurements will be given for some specimens: —

| Measurements<br>in mm | RM Ec<br>5058 | RM Ec<br>5038 | RM Ec<br>5052 | RM Ec<br>5037 | RM Ec<br>5063 | RM Ec<br>5041 | RM Ec<br>5040 | RM Ec<br>5051 | RM Ec<br>5056 | RM Ec<br>5066 | RM Ec<br>5053 |
|-----------------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|
| Height of theca       | 5.5           | 6.8           | 6.8           | 8.0           | 8.5           | 9.0           | 9.2           | 10.0          | 12.0          | 12.0          | 17.0          |
| Greatest diam.        | 4.5           | 4.8           | 5.8           | 6.2           | 7.0           | 7.5           | 8.7           | 10.0          | 11.0          | 10.2          | 14.0          |

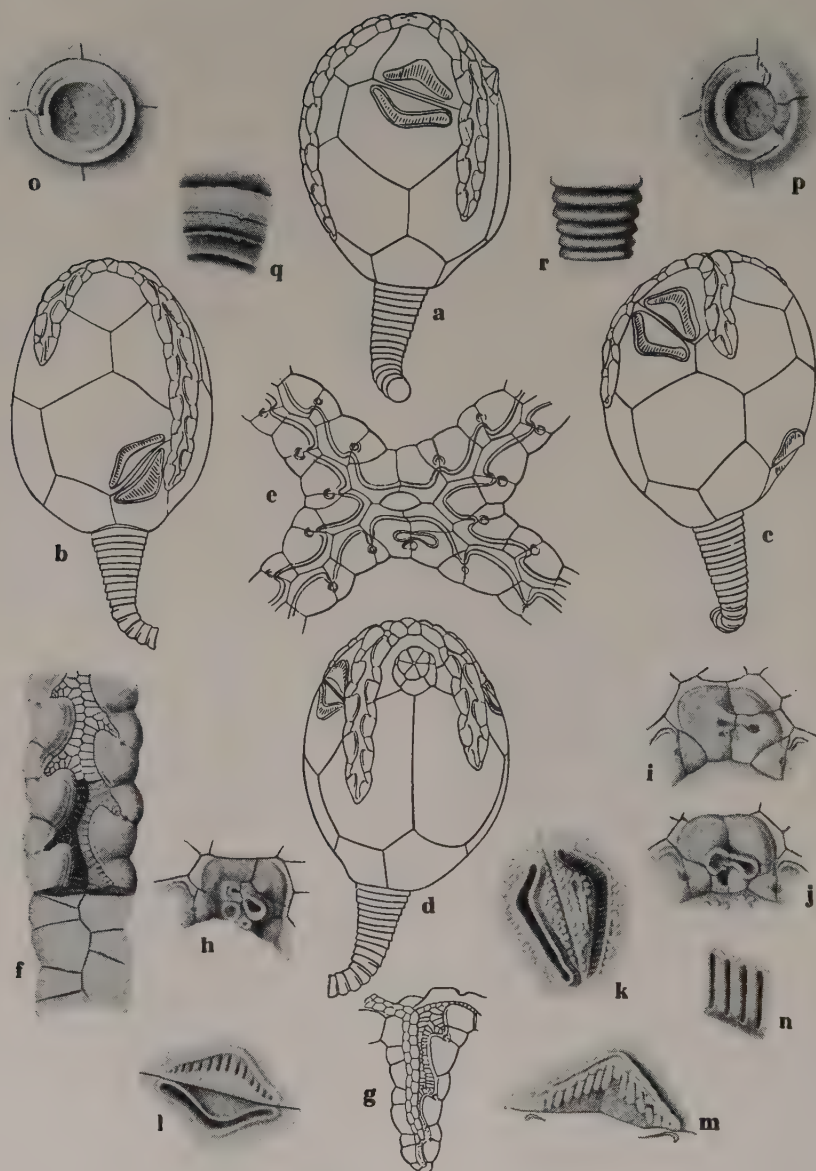
As to the thecal skeleton may further be referred to text-fig. 16: a—d. It should be remarked that the skeleton elements of the very apical region are concealed by the ventral portions of the ambulacra and connected so intimately with those that no clear idea of their arrangement was obtained even after preparing away the ambulacra.

The pectinirhomb, as is natural, are less developed in immature specimens. In the specimens RM Ec 5058 and 5037, the measurements of which are contained in the above table, the number of pores on each side of the pectinirhomb is respectively: — basal pectinirhomb: 3—4; 7; *L* 1—*R* 5 pectinirhomb: 8—9, 11; *L* 4—*R* 3 pectinirhomb: 12, 13. The last-mentioned is always best developed, whereas the basal rhomb is smallest. The stereom bridge interrupting the pore-folds is usually wider in large specimens. Thus with increasing age the whole rhomb becomes wider.

Ambulacral system. In small specimens the ambulacra are concentrated to the apical area. During the development of the specimen the ambulacra grow downwards towards the base, which is in certain specimens reached by some of the ambulacra or all of them. No plan regulating the increase of the ambulacra could be stated from the material available. In RM Ec 5053, e.g., the ambulacrum of radius I is the only one that reaches the *B*-circlet, whereas in RM Ec 5068 the corresponding ambulacrum is the only one not reaching the *B*-circlet. In RM Ec 5066 the ambulacra of radii V and I reach this level, and so on. — The delicate details in the construction of the ambulacra are usually not recognizable. The minute flooring plates illustrated in text-fig. 16: f, g, can be traced in e.g. RM Ec 5041. Covering plates have been detected only in RM Ec 5035 (text-fig. 16: g). The number of brachiole-facets stands of course in relation to the length of the ambulacrum.

The plate (*O* 1), in which the hydropore and the gonopore open, seems to be divided in two parts by a suture sectioning the said pores (text-fig. 16: e, h—j). In RM Ec 5041 (text-fig. 16: h) this has led to a dividing of the canal of each of these organs, so that they open with two pores.

The anus was covered by a pyramid, which is seldom preserved. In RM Ec 5035 six valvulae are present (cf. text-fig. 16: d; ANGELIN 1878 a, Pl. 19, fig. 18 a). Between the anal aperture and the surrounding thecal plates there is a dorso-lateral border of small plates, 5—6 in number. It



Text-fig. 16. *Lovénicystis angelini* (JAEKEL). a—d Restored specimen in different views [composed of details from RM Ec 5039 (the stem), RM Ec 5040 ?, RM Ec 5035 ?]. e Circumoral ambulacral area. f Detail of ambulacrum. g A short ambulacrum showing covering and flooring plates of the groove [RM Ec 5035]. h Hydropore and gonopore, with two openings each [RM Ec 5041]. i—j Hydropore and gonopore. k, l [RM Ec 5041], m [RM Ec 5035], n [RM Ec 5034 ?] Pectinirrhombs. o, p [RM Ec 5040] Base of the theca with proximal columnal. q Probably section through the test. r Detail of stem. (From LOVÉN MS, Pl. 13; lettering by the present writer.  $\frac{2}{3}$  of original size).

should be noted that the space between the anus and the ambulacral plates above is usually not as great as indicated in text-fig. 16: d.

A complete stem has not been found in connexion with the theca, the specimen figured by LOVÉN (our text-fig. 16: a—d) being restored. In reality the stem (drawn from RM Ec 5039 labelled "Rikvide") is isolated but may be supposed to belong to this species, which cannot be ascertained, however. A number of stem-fragments [RM Ec 5099] recalling in appearance the mentioned stem are more doubtful, since they might originate from a somewhat lower horizon, being collected at Djupvik, in the parish of Eksta.

As to the systematic status of *Lovénicystis angelini* may be referred to the above discussion of the relations of the genus.

**Regional distribution:** — Sweden, Gotland: Lau (this locality is indicated for a few specimens only, the main part being labelled "Gotland"; cf. p. 92, foot-note 20) (? Hablingbo, Rikvide, ?? Djupvik: stem-fragments).

**Stratigraphic range:** — (?? Mulde marl-) Eke group, (?? uppermost Wenlock-) Lower Ludlow (cf. the foot-note just referred to).

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The families to follow below are those comprised in the group Irregularia of JAEKEL (1899, 1918). In the introductory remarks on the order Rhombifera (p. 68 above) it was mentioned that the divisions Regularia and Irregularia should not be maintained. Yet it might be suitable to adopt the subdivisions of the Irregularia proposed by JAEKEL in 1918, which seem to be well founded. Only the names will be modified.

In 1918 JAEKEL ranked the Irregularia (as well as the Regularia) as an order. Three suborders were recognized, viz. Hemicosmites, Polycosmites, and Caryocystites. These designations being homomorphous with (at least partially) wellknown generic names, the present writer — ranking as super-families the taxonomic units to which they apply — suggests to change the given names into Hemicosmitida, Polycosmitida, and Caryocystitida.

### Superfamily **Hemicosmitida** (JAEKEL 1918) n. nomen.

In describing the species of genera belonging to the Hemicosmitida, the present writer arrived at the decision to use, for the sake of convenience, the terms *BB* for the plates of the lowest thecal circlet, and so on, in accordance with JAEKEL. But we must realize that the homologies of the different thecal elements are not beyond discussion. This is evident from the interpretations presented by various authors. Thus CARPENTER (1891, p. 2 seq.) advanced the opinion that the dorsal skeleton in these forms



— as well as in several other hydrophorid genera — is comparable to that of a crinoid with dicyclic base. This view was adopted by BATHER (1900, pp. 65—66; 1906, p. 27), whereas JAEKEL (1899, pp. 293, 305—307; 1918, p. 97) gave another interpretation, as just mentioned. Their different conceptions appear from the following comparison: —

| JAEKEL            | BATHER                     |
|-------------------|----------------------------|
| Radiolateralia    | Deltoidea                  |
| Mediolateralialia | Radialia (+ Interradialia) |
| Infralateralia    | Basalia                    |
| Basalia           | Infrabasalia               |

In a paper of 1910 BATHER, "to avoid confusion" (p. 39; p. 4 of separate print), chose to denote the circlets of the theca by the indifferent numerals I—IV, I being the lowest circlet. This does not seem to be necessary, however, after the reader's attention has been called to the fact.

#### Family **Hemicosmitidae** JAEKEL 1918.

##### Genus ***Hemicosmites*** BUCH 1840.

Genotype: — *Hemicosmites pyriformis* BUCH 1840.

Synonyms: — See JAEKEL 1899 (p. 307).

Regional distribution: — ? France (Lower Ordovician),<sup>21</sup> USSR, Estonia, Sweden, Norway, ? Britain (all Middle Ordovician),<sup>22</sup> China (Middle and ? Upper Ordovician),<sup>23</sup> ? S. Africa.<sup>24</sup>

Stratigraphic range: — ? Lower Ordovician, Middle Ordovician, ? Upper Ordovician.

For diagnosis and general discussion of the genus may be referred to JAEKEL 1899 (p. 307 seq.) and 1918 (p. 97).

The only previous announcement of *Hemicosmites* from Sweden was made by THORSLUND (1936, p. 26), who reported the genus from the Kullsbjerg limestone of Dalarna.

<sup>21</sup> THORAL 1935 a, p. 159.

<sup>22</sup> N.B. the observations of JAEKEL (1899, pp. 314—315) on the species described by FORBES (1848, pp. 510—511) under the name of *Hemicosmites*.

<sup>23</sup> From the Middle Ordovician of Kweichow SUN (1936, p. 481) reported *Hemicosmites jækeli* SUN 1936. About the Upper Ordovician *Hemicosmites ? loczyi* Jaekel 1899, see BATHER 1906, p. 29.

<sup>24</sup> In giving the distribution of the family Hemicosmitidae, JAEKEL (1918, p. 97) mentioned also "Reste fraglicher Stellung auch aus Ostchina und Südafrika". The present writer did not succeed to find out the base for the last-mentioned statement.

*Hemicosmites oelandicus* n. sp.

Pl. 3, fig. 12.

Derivation of name: — After the island of Öland.

Holotype: — RM Ec 4362.

Type locality: — Böda, Öland.

Type stratum: — Lower Chasmops limestone, Middle Ordovician.

Material: — One undisputable specimen only, the holotype; the actinal region is unfortunately imperfect. A poorly preserved *Hemicosmites* [SGU] from the Lower Chasmops limestone of Älleberg, Västergötland, is possibly referable to this species. Unfortunately the imperfect state of preservation renders a closer examination of the specimen fruitless.

Diagnosis: — A species of *Hemicosmites* with globular theca; profile-line of *BB* almost straight or but very slightly concave; all *ILL*, except *IL 5*, as wide as high; no concentric plate ornament; nodes on *ILL* hardly recognizable or lacking.

Description: — General shape of the theca. The theca is almost spheroidal, as appears from the following

measurements. Height 26.7 mm; diameter (measured in the height of the anus) 25.6 mm, which means a height-width ratio of 1.04.

Thecal skeleton. The theca is constructed according to the regular plan of the genus. The relative width of the thecal plates is rather great, being a function of the relatively great diameter of the theca. As mentioned in the diagnosis, most *ILL* are as wide as high, *IL 5* only making an exception. In this plate the height is 14 mm and the width 10.5 mm.

Surface structures of stereom. The plates are devoid of any well-defined ornament, except a node on each *L* below a brachiole-facet, and the small protuberances — very little prominent indeed — being pierced by the thecal pores. Besides that the plate surfaces are somewhat uneven.

Pores of the thecal plates. The pores, of the appearance described by JAEKEL (1899, p. 298 seq.) are not very conspicuous and seem to be rather irregularly distributed.

The ambulacral area is, as mentioned, not preserved well enough to demonstrate any details. The brachiole facets can only be traced. A hydropore has never been recognized in the genus (JAEKEL 1899, p. 298).

Alimentary canal. In consequence of the bad state of preservation of the oral pole, the mouth is not visible. The small circular anus (diam. 3 mm) is located in the limit between *IL 5* and the anal plates *L a* and *IL a*; its valvulae are not preserved.

The gonopore is not traceable.

The stem is wanting. Its diameter at the base of the theca was about

3 mm. Here it was surrounded by a quadrangular rim formed by basal swellings on the *BB*.

**Discussion:** — This species belongs to a group of forms with approximately globular theca. The other members are *Hemicosmites malum* (PANDER 1840), *H. pyriformis* BUCH 1840, and *H. laevior* JAEKEL 1899. Their relations to our species will be reviewed.

The two first-mentioned were often thought to be identical, and the supposed species has been referred to sometimes under the name given by PANDER, and sometimes under the name given by BUCH. JAEKEL (1899, p. 309) held them apart, which is no doubt justified.

*Hemicosmites malum* (East Baltic area; stratigraphic appearance not closely known, according to JAEKEL 1899, p. 309, stage  $C_1$ ) differs from the Öland form in the lower position of the anus (in the limit between *IL 5* and *IL a*), in having nodes on the *ILL*, and in having a concentric ornament on the thecal plates. *Hemicosmites laevior* seems to differ from the preceding species by minor size and less development of the nodes on the thecal plates. Its occurrence and age are not closely known (JAEKEL l.c.). *Hemicosmites pyriformis*, finally, was well described by BUCH (1846 a, p. 108; 1846 c, p. 34).<sup>25</sup> It was reported from USSR and Estonia. Neither BUCH nor other writers have given a definite statement of its geologic horizon, however. A form determined as *Hemicosmites pyriformis* ? was later mentioned from Norway (KJERULF 1865, p. 4; BRÖGGER 1882, p. 42). The holotype (in the Berlin museum) was refigured by JAECKEL (1899, Pl. 17, figs. 6 a—b). It is more oval (the height-width ratio 1.1 against 1.04 in our species), and the profile-line of the *BB* is markedly curved inwards. The relative width of the *ILL* is less than in *Hemicosmites oelandicus*. Height and width of *IL 5* are in our specimen 14 mm respectively 10.5 mm (ratio=1.33). Corresponding measurements (taken from JAEKEL's figure) is in the holotype of *Hemicosmites pyriformis* 12.2 mm and 9 mm (ratio=1.47). In the mentioned species the concentric ornament and the pore-lines are well marked.

**Regional distribution:** — Sweden, Öland: Böda. — (? Västergötland: Älleberg).

**Stratigraphic range:** — Lower Chasmops limestone, Upper Llandeilian.

### *Hemicosmites extraneus* EICHWALD 1840.

Pl. 3, figs. 13—14.

1840 *Hemicosmites extraneus* m. — EICHWALD, p. 194 (p. 182 of Germ. ed.).

1845 *Hemicosmites pyriformis*. — VERNEUIL, p. 31, Pl. 1, figs. 3 a—c.

<sup>25</sup> The actinal region was misinterpreted and was illustrated wrongly in BUCH's figures. The mistake was corrected by MÜLLER (1854, p. 180), who communicated nice figures (MÜLLER, Pl. 6, figs. 4—5) of a specimen in apical view.



- 1856 *Hemicosmites extraneus*. — EICHWALD, p. 124.  
 1860 *Hemicosmites extraneus* m. — EICHWALD, p. 634, Pl. 32, figs. 5 a—c.  
 1899 *Hemicosmites extraneus* EICHWALD. — JAEKEL, p. 310.  
 1911 *Hemicosmites extraneus* EICHWALD. — BASSLER, p. 20.  
 1928 *Hemicosmites extraneus* EICHW. — SCUPIN, p. 172.

**H o l o t y p e:** — Unknown to the present writer. The original description was not accompanied by any figure.

**T y p e l o c a l i t y:** — Spitham, Estonia.

**T y p e s t r a t u m:** — Stage  $D_3$  (Wasalemm), according to BASSLER (1911, p. 20) and SCUPIN (1928, p. 172);  $D_1$  (Jewe), according to JAEKEL (1899, p. 310) Middle Ordovician.

**M a t e r i a l:** — Four specimens are available [RM Ec 2278, 2280, 2281, UM ec 95], somewhat worn but otherwise mainly well preserved.

**D e s c r i p t i o n:** — General shape of the theca. The theca is oval, tapering a little more downwards than upwards. As far as general conclusions can be drawn from the small material at hand, the relative width decreases with increasing age and size of the specimen. The following table will demonstrate this.

| (Measurements in mm)           | RM Ec 2278 | UM ec 95 | RM Ec 2280 | RM Ec 2281 |
|--------------------------------|------------|----------|------------|------------|
| Height of the theca .....      | 39.5       | 29.0     | 27.0       | 23.0       |
| Diameter in height of the anus | 28.6       | 21.9     | 21.4       | 18.4       |
| Height-width ratio .....       | 1.38       | 1.32     | 1.26       | 1.25       |

The thecal skeleton shows no divergences in construction from the plan characteristic of *Hemicosmites*. No *IL* is as wide as high.

**S u r f a c e s t r u c t u r e s o f s t e r e o m.** One longitudinally elongated node is present on each *L* situated below a brachiole-facet. Small tubercles are developed occasionally on other *LL* too. A weakly defined concentric ornament can be traced in RM Ec 2278 but hardly in the other specimens. The thecal pores are surrounded by rims.

**P o r e s o f t h e t h e c a l p l a t e s.** The regular, disjunct pore-rhombs are confined mainly to *LL* and *ILL*. On *RR* and *BB* pores are not so frequent and seem to be more irregularly distributed. In consequence of irregular weathering different levels of the plates are exposed to view, and according to this the appearance of the pores varies. Thus all types illustrated by JAEKEL (1899, text-fig. 68: b—e, p. 299) are visible.

The ambulacral area, with 3 brachiole-facets, shows no remarkable peculiarities.

**A l i m e n t a r y c a n a l.** The mouth is covered by an apical pavement of small plates. The rounded anus opens between *IL* 5 and the anal plates *La* and *ILa*. Its diameter varies between 3 and 4.5 mm, according to the size of the theca. The anal pyramid is not preserved in any specimen.

The gonopore is visible in UM ec 95. It is a very small opening located in the upper suture of the interambulacral *R* above the anus, as observed by JAEKEL (1899, p. 298).

The stem is not preserved in any specimen available but for the proximal columnal in the specimen just referred to. At its point of attachment to the theca the stem was surrounded by a rim, formed by basal swellings on the *BB*. It was very feeble, the diameter being in the largest specimen 4 mm only. In UM ec 95 the diameter of the proximal columnal is about 3 mm. The walls are thick so that the diameter of the lumen does not exceed 1 mm.

**Discussion:** — The Swedish specimens here under consideration agree in all essentials with *Hemicosmites extraneus* as described and figured in the papers quoted above in the list of synonyms, and with East Baltic material available to the writer. The only difference is that in our specimens the concentric ornament of the thecal plates is but very faintly indicated or totally lacking. It is obvious, however, that surface structures of the stereom are recognizable in unworn specimens only. This feature, therefore, need not prevent us from an unreserved identification.

The only species hitherto described, for which *Hemicosmites extraneus* could be mistaken, is *Hemicosmites pulcherrimus* JAEKEL 1899. This species is characterized by a pretty developed surface ornament; the relative width of the theca seems to be somewhat minor than in *Hemicosmites extraneus*.

**Regional distribution:** — Sweden, Dalarna: Kullberg. — Estonia. — USSR.

**Stratigraphic range:** — The Swedish specimens are from the Kullberg limestone, i.e. the lower section of the reef-limestone formerly known as "Leptaena limestone". It falls within the upper part of the Chasmops series and the basal Tretaspis series, corresponding in age to the topmost Llandeillian and part of the Caradocian.

As mentioned above (p. 101), statements concerning the stratigraphic appearance of *Hemicosmites extraneus* in the East Baltic area are not univocal. Anyhow it occurs in strata equivalent to the Kullberg limestone.

### Family **Caryocrinitidae** (BERNARD) BASSLER 1938.

#### Genus **Caryocrinites** SAY 1825.

**Genotype:** — *Caryocrinites ornatus* SAY 1825.

**Synonyms:** — See BASSLER 1938 (p. 61).

**Diagnosis:** — See JAEKEL 1899 (p. 313) and BATHER 1906 (p. 28).

**Remarks:** — A survey of the genus *Caryocrinites* was given by BATHER 1906 (pp. 28—29). The known species were divided into two series,

one "normal series resembling *C. ornatus* in the possession of ridges which radiate from the umbones of the cup-plates and are bordered by pores", and one "*Stribalocystis* series, as one may conveniently term it, with ridges absent or merged in the general shape of the plates, and with pores often obscure". Accordingly, *Stribalocystites* S. A. MILLER 1891 was here included in *Caryocrinites*. The same position was held by BATHER 1900 (p. 67). In 1899 (p. 312—313) JAEKEL was in doubt of its rank, and in 1918 (p. 98) he placed it tentatively in fam. Hemicosmitidae. BASSLER (1938, p. 176) regarded *Stribalocystites* as a separate genus. There is no need further to discuss the question here, since the inconsiderable Swedish material is referable to BATHER's "normal" series.

**Regional distribution:** — Burma (Middle Ordovician), Sweden (Upper Ordovician), Norway (basal Silurian), N. America (Middle Silurian).

This genus, known from of old, was for a long time thought to be exclusively American. The announcements of *Caryocrinites* from Sweden by HOLM (1890, p. 268) and from Norway by KIAER (1897, pp. 17, 75) were not observed by JAEKEL, who stated (1899, p. 150) that the genus is confined to North America (p. 303 he declared expressly that the "Caryocrinidae" — in which *Hemicosmites* also was comprised — are entirely absent in Swedish strata). BATHER (1906, p. 29) called attention to the Scandinavian finds.

**Stratigraphic range:** — Middle Ordovician — Middle Silurian.

### *Caryocrinites septentrionalis* n. sp.

Pl. 3, fig. 15. Pl. 4, fig. 1.

1890 "*Caryocrinus* mycket närstående *C. ornatus* SAY." — HOLM, p. 269 (15).

**Derivation of name:** — From Lat. *septentrionalis*, northern.

**Holotype:** — The specimen figured in our Pl. 3, fig. 15 [SGU].

**Type locality:** — Well in the SW slope of Lissberg, Gulleråsen, Dalarna.

**Type stratum:** — Red marl-shale, probably equivalent to the lower part of the Boda limestone, Tretaspis series, Upper Ordovician.<sup>26</sup>

**Material:** — The only theca available is the holotype; in the same glass-tube as the holotype is a stem-fragment, which possibly belongs here; other similar stems are in LM and RM.

**Diagnosis:** — A species of *Caryocrinites* with small theca with sub-parallel sides; axial ridges of thecal plates little pronounced, bordered by pores or with a single row of pores; anus entirely within the tegmental

<sup>26</sup> According to kind information by Dr P. THORSLUND (letter to the author).

portion of the theca; brachiole-facets stout and somewhat projecting, being located close above the umbo in the *LL*; tegminals stout.

**Description:** — The general shape of the theca is approximately ovoid, the widest portion being in the transversal plane sectioning the umbos of the *ILL*. Below this plane the theca tapers towards the flattened base. Above the same plane the sides of the theca are sub-parallel, converging but slightly. On account of the stoutness of the plates supporting the brachiole-facets and of the tegminals the upper part of the theca obtains a decidedly bumpy appearance. — The tegminal area is flattened.

**Measurements.** Height 21 mm; sagittal equatorial diameter 17.8 mm; transversal equatorial diameter 19 mm.

**Thecal skeleton.** The construction of the theca is that characteristic of *Caryocrinites*, with 4 *BB*, 6 *ILL*, and 8 *LL*. The number of plates in the fourth circlet cannot be made out safely, for the sutures are not distinct, but might be 12—13. Further there are 5—6 tegminal plates. — The plates of the different circlets show no peculiarities but are quite normal.

**Surface structures of stereom.** In the *ILL* and in the lower halves of the *LL* slightly pronounced axial ridges radiate from the umbo to the angles of the plates. Such structures cannot be detected in the *BB*, at least not in *B 3* and *B 4*; *B 1* and *B 2* may each have two very faintly indicated ridges. In the *ILL* the umbo is provided with a knob, as a rule knocked off in the actual specimen. A central tubercle is also visible in certain plates of the ventral area. The surface of all plates is finely shagreen-like.

**Pores of the thecal plates.** The axial ridges on *ILL* and *LL* are bordered by pores on tubercles. Occasionally only a single row of pores is visible, *B 3* and *B 4* seem to be devoid of pores, whereas such are developed in *B 1* and *B 2*.

**The ambulacral grooves** are not exposed to view, being protected by covering plates. The brachiole-facets — close above the umbos of the *LL* — are not quite distinct; their number is probably nine. A hydrepore is not visible.

**Alimentary canal.** Along with the ambulacral grooves the mouth is covered by plates. The circular anus seems to be surrounded by three plates and is situated entirely within the ventral surface. Its diameter is 3 mm. The anal pyramid is not preserved.

A gonopore cannot be traced.

In the holotype nothing is preserved of the stem. In the base there is a circular depression — 2.5 mm in diameter — between four basal



swellings on the *BB*. Whether the stem-fragment associated with the holotype really belongs to this species can of course not be decided. Yet this and a few other fragments remind of the stem in *Caryocrinites ornatus* as figured by HALL 1852 (Pl. 49, figs. 1 a, 1 d, 1 z). Therefore they may be referred tentatively to the present species. In the specimen reproduced in our Pl. 4, fig. 1, there are 6 columnals in 10 mm.

**Discussion:** — The relations of *Caryocrinites septentrionalis* to other congeneric forms will be reviewed shortly.

Exclusive of the Silurian North American species, only a few representatives of this genus are known. The oldest one is *Caryocrinites aurora* (BATHER 1906) from the Shan States, Burma (BATHER 1906, p. 29; ? REED 1936, p. 12). A few other species described by BATHER (1906) under the name of "*Caryocrinus*" belong to *Stribalocystites*. The position of Upper Ordovician forms of "*Caryocrinus*" mentioned by REED (1932, p. 201) from the Southern Shan States is uncertain.

*Caryocrinites aurora* originates from the Naunkangyi beds, which were said by REED (1906, p. 85) to be equivalent to "the Cystidean or Echinospaerite Limestones of Scandinavia and Russia", i.e. Upper respectively Middle Llandeilian. From our specimen it differs in the following respects: — theca larger, tapering towards the oral pole; relative width of the plates minor (height-width ratio 1.6 for *IL* 5 compared with 1.3 for the same plate in the Swedish specimen); brachiole-facets not projecting; tegminals not stout.

As to a Swedish form from the same locality as *Caryocrinites septentrionalis* but probably distinguished specifically, cf. below.

The Norwegian species from stage 5 b (basal Silurian) in Ringerike, mentioned by KLÆR (1897, pp. 17, 75) as "*Caryocrinus* sp.", has unfortunately not been described. According to KLÆR only one specimen has been met with.

All other known species are from the Middle Silurian of N. America. Of these *Caryocrinites ornatus* SAY 1825 differs in a higher position of the brachiole-facets but a lower one of the anus; the theca is usually larger and does not present the bumpy appearance of the ventral portion characteristic of our species. About the same may be said of *Caryocrinites milliganae* (MILLER & GURLEY 1896) [Synonyms: — *C. hammeli* (MILLER & GURLEY 1896), fide BATHER 1906, p. 28, and *C. roemeri* (JAEKEL 1899), fide BATHER l.c. and BASSLER 1915, p. 187].

*Caryocrinites missouriensis* (ROWLEY 1900) has a small theca but differs by strongly developed ornament on the plates.

*Caryocrinites ellipticus* (MILLER & GURLEY 1894), finally, which should be termed *C. gorbyi* (MILLER & GURLEY 1892) if BATHER's proposition (1906, p. 28) is correct that this form is the young of the species later called

*ellipticus*, reminds in certain respects of our species. Size and shape of the theca are tolerably the same, though the theca is more pronouncedly ovoid in the American form and is somewhat more elongate. It differs, however, i.a. by strong ornament on the plates, also on the *BB*, and by not projecting brachiole-facets.

The Middle Ordovician *Caryocrinites aurora* displays certain characters approaching it to *Hemicosmites*, as pointed out by BATHER (1906, p. 29), viz. the slight development of the tegmen and the nature of the brachiole-facets, which are excavated. These primitive features have disappeared already in our Upper Ordovician species.

**Regional distribution:** — Sweden, Dalarna: Lissberg of Gulleråsen (? Arvet, Boda: stem-fragments).

**Stratigraphic range:** — Tretaspis series, Ashgillian.

### *Caryocrinites?* sp.

Pl. 4, fig. 2.

**Locality:** — Lissberg, Gulleråsen, Dalarna.

**Stratum:** — Red marl-shale, presumably the same as the type stratum of the preceding species, i.e. a horizon probably equivalent to the lower part of the Boda limestone, Tretaspis series, Upper Ordovician.

**Material:** — One isolated thecal plate only, lying in a piece of rock [LM]. Probably it is an *IL*.

**Remarks:** — Although originating from the same locality as *Caryocrinites septentrionalis* n. sp. the present specimen might hardly be referable to that species. It differs by its strongly pronounced axial ridges well elevated over the general surface of the plate and bordered by pores. Further its size is by far greater than in any plate of *Caryocrinites septentrionalis*, the diameters being about  $18.5 \times 18.5$  mm, compared with  $10 \times 10$  mm for an *IL* in that species. The edges of the plate are not well defined but it seems to have been heptagonal in outline. This would indicate that the plate represents *IL* 1 or *IL* 3.

In size and character of the stereom structures the present specimen approaches species such as *Caryocrinites ornatus* and *Caryocrinites milliganæ* more than does *Caryocrinites septentrionalis*.

Finally, it should be pointed out that an arrangement of the pores similar to that of our specimen is to be found in certain species of *Hemicosmites* also, though more characteristic, on the whole, of *Caryocrinites*. It might be convenient, therefore, to refer it to the last-mentioned genus with a mark of interrogation.

Superfamily **Polycosmitida** (JAEKEL 1918) n. nomen.

Family **Stichocystidae** JAEKEL 1918.

Genus ***Stichocystis*** JAEKEL 1899.

**Genotype:** — *Caryocystis geometrica* ANGELIN 1878.

**Synonyms:** — *Caryocystis* (ex parte) ANGELIN 1878 a. — *Heliocystis* (ex parte) HAECKEL 1896. — *Caryocystites* (ex parte) JAEKEL 1899.

**Diagnosis:** — Coincident with that of the family ("Poren in radialen Leisten angeordnet". JAEKEL 1918, p. 98).

**Remarks:** — This genus was originally (JAEKEL 1899) placed with *Caryocystites* (including *Heliocrinites*), *Echinosphaerites*, and "*Amorphocystis*" (i.e. *Caryocystites*) to constitute the family "Echinosphaeridae", *Stichocystis* being looked upon as its most primitive member. This assumption implies, however, that the oldest forms of *Stichocystis* are undiscovered as yet, for the only species known might not have appeared earlier than the other genera concerned.

*Stichocystis* was retained in the Echinosphaeritidae by BATHER (1900, p. 55; 1906, p. 15), SPRINGER (1913, p. 152) HECKER (1923, p. 47), ZITTEL-BROILI (1924, p. 215), SUN (1936, p. 483), and BASSLER (1938, p. 175). In the revision of his system, JAEKEL (1918, p. 99) found no place for *Stichocystis* in the new suborder Caryocystites (=superfamily Caryocystitida of the present paper; with the families Caryocystitidae and Echinosphaeritidae), but ranged it — along with *Polycosmites* JAEKEL 1918 — as a separate suborder (=superfamily Polycosmitida of the present paper). This arrangement was dictated by the conception that the two genera mentioned hold an intermediate position between the Hemicosmitida and the Caryocystitida with regard to pore-structure. It is true that *Stichocystis* comes very close in habit to certain representatives of *Heliocrinites* and may even be mistaken for a species of *Heliocrinites* in cases where delicate details are not recognizable. But in the author's opinion the differences in pore-structures are so important as to justify the classification proposed by JAEKEL.

**Regional distribution:** — Sweden, Germany (drift boulders), China.

**Stratigraphic range:** — Middle Ordovician.

***Stichocystis geometrica*** (ANGELIN 1878).<sup>27</sup>

Pl. 4, figs. 3—4.

1878 *Caryocystis geometrica* ANG. — ANGELIN 1878 a, Pl. 12, figs. 22—24. (No description was given).

<sup>27</sup> The species was designated by JAEKEL (1899, p. 327) as "n. sp.", ANGELIN's name being given within brackets. According to article 21 of the international rules of zoological

1896 *Heliocystis* (*Heliocrinum*) *geometrica* ANGELIN. — HAECKEL, p. 58.

1899 *Stichocystis geometrica* (ANG.) n. sp. — JAEKEL, p. 327, Pl. 9, fig. 6.<sup>28</sup>

**Holotype:** — RM Ec 5543, a fragment of the test seen from the inside.

**Type locality:** — Not known, the holotype being collected in a drift boulder (Stralsund, Germany).

**Type stratum:** — Not known with certainty. JAEKEL (1899, p. 327) described the rock bearing *Stichocystis* as "Backsteinkalk". If originating from Sweden, the piece of rock containing the holotype is most likely to have been derived from the Chasmops limestone (Upper Llandeilian) as far as can be inferred from its lithological character.

**Material:** — The holotype and 3 more specimens in RM, tolerably well preserved.

**Diagnosis:** — A species of *Stichocystis* with rounded theca; pore-lists widely separated, straight, and rigorously parallel, thus producing a regular ornament.

**Description:** — General shape of the theca. In shape the theca might have been spheroidal with slightly protruding ambulacral area. JAEKEL (1899, p. 326), in the diagnosis of the genus, suggested the area bearing the brachioles not to be elevated over the general surface of the theca, but he might not have had at his disposal specimens showing the actual state. It is true, however, that the ambulacral eminence is considerably less conspicuous than in many *Caryocystitida*.

| (Measurements in mm)      | RM Ec 2282 | RM Ec 2283 | RM Ec 2279 |
|---------------------------|------------|------------|------------|
| Height of the theca ..... | 41         | 27         | 20.7       |
| Greatest diameter .....   | 43         | 29         | 18.3       |

**Thecal skeleton.** As observed by JAEKEL (1899, p. 326), the plates are amalgamated very intimately so that the sutures are generally not recognizable. In the largest of the specimens available the number of plates seems to be 50—60, whereas in the smaller specimens it is considerably smaller. The plates are mainly hexagonal.

**Surface structures of stereom.** The sutures are crossed at right angles by 1—5 low ridges. These ridges are widely apart and

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nomenclature, the person is to be reckoned as author of a scientific name, who was the first to publish it "in Begleitung einer Indikation, einer Definition oder einer Beschreibung". The plain figures communicated by ANGELIN seem to be a sufficient indication. ANGELIN, therefore, is taken as author of this species.

<sup>28</sup> JAEKEL referred also to ANGELIN's Pl. 13, figs. 14—16, and Pl. 14, figs. 22—28, as belonging to this species, an assumption which is avoid of all foundation and might be due to a lapsus calami.



rigorously parallel. There is as a rule one longer ridge flanked by shorter ones. The centres of the plates are generally not elevated so as to project as umbos.

**Pores of the thecal plates.** The ridges mentioned are pierced by a series of pores, which are not always visible in our specimens. The number of pores in the single ridges is, of course, conditioned by the length of the ridge in question. More than 15 pores in a ridge were not ascertained but a greater number might occur in especially long ridges. In most cases the number is considerably smaller.

The ambulacral area is in RM Ec 2282, where the structures are still traceable, approximately semilunar and measuring  $10 \times 7$  mm. Seemingly, 5 brachiole-facets have been present. — No gonopore was detected.

**Alimentary canal.** The mouth is a narrow slit elongated transversally [RM Ec 2279]. An elevation visible in RM Ec 2282 below the straight side of the ambulacral area and situated somewhat above the equatorial plane, might represent a pyramid covering the anus.

On the right side close to a line connecting the mouth and the supposed anus there is in the latter specimen a thick-walled aperture, having a length in transverse direction of about 2 mm. It is not situated midway between the endpoints of the alimentary canal but is a little closer to the mouth. By analogy with the conditions in e.g. *Caryocystites* we may interpret this opening as a gonopore (cf. p. 115, foot-note 29).

The stem is not preserved. But it can be inferred from the cicatrix that it was exceedingly feeble. In the largest specimen its diameter is about 3.5 mm only. It lies here somewhat before the aboral pole.

**Discussion:** — The three specimens in hand do not show any specific differences from *Stichocystis geometrica* on comparison with the imperfect holotype and the description delivered by JAEKEL. *Stichocystis* sp. described and figured by SUN (1936, p. 483, Pl. 1, fig. 3) was said to agree with the type species as far as could be inferred from the small fragment, which does not admit of a safe specific determination.

**Regional distribution:** — Sweden, Dalarna: Kullsberg. — Northern Germany (drift boulders). — ? China.

**Stratigraphic range:** — The Swedish specimens were collected in the Kullsberg limestone, which falls within the upper part of the Chasmops series and the lowest part of the Tretaspis series (Upper Llandeilian—Middle Caradocian). It was already mentioned above that the rock of the holotype indicates an age agreeing with that of the lower part of the Kullsberg limestone.

*Stichocystis alutacea* (ANGELIN 1878).

Pl. 4, fig. 5.

1878 *Caryocystis alutacea* ANG. — ANGELIN 1878 a, p. 29, Pl. 13, figs. 10—13.1888 *Caryocystis alutacea* A. — LINDSTRÖM 1888 a, p. 16.1896 *Heliocystis (Heliopirum) alutacea* ANGELIN. — HAECKEL, p. 59.1899 *Caryocystites alutacea*. — JAEKEL, p. 339, Pl. 8, fig. 21.

**Holotype:** — RM Ec 2753, a partly imperfect mould, the details of which are obscure to a great extent.

**Type locality:** — Jonstorp (Mösseberg), Västergötland.

**Type stratum:** — Probably Chasmops limestone, Middle Ordovician. Since the specimen is isolated without any detached rock-fragments, no definite opinion of its origin can be given.

**Material:** — One specimen only, the holotype.

**Diagnosis:** — A species of *Stichocystis* with elongated theca; pore-lists crowded.

**Description:** — General shape of the theca. The theca is elongated, sack-like, with irregular outline, so that it appears rather different from varying aspects. The oral region is unfortunately damaged.

**Measurements:** — Height 47.2 mm; largest diameter 30 mm.

The thecal skeleton is composed of large plates rather irregular in outline. They are arranged in circlets which are not clearly defined, however, but interlock in many instances. This is due to the irregular size and shape of the plates. An analysis of the theca — such as that communicated by ANGELIN (1878 a, Pl. 13, fig. 13) — can hardly be performed in detail on basis of the holotype. According to ANGELIN's fig. just quoted there would be 46 plates arranged in 6 irregular circlets. As to the general arrangement of the plates, ANGELIN's representation could be mainly confirmed, however, but for the oral region, the construction of which cannot be deciphered. No more than about 40 thecal plates seem to be recognizable.

The surface structures of the stereom are not visible in the present mould. JAEKEL's figure (1899, Pl. 8, fig. 21) shows rhombs of fine and densely set pore-ridges (13 in the rhomb in the middle of the fig.).

**Pores of the thecal plates.** The typical *Stichocystis*-structure shows itself in the lines of small tubercles disposed in rhombic areas, corresponding to the extension of the pore-lists. These tubercles are casts of the vertical pore-canals. Often, and especially in the neighbourhood of the sutures, they are somewhat elongated, representing a more or less oblique section through the pore-canal. The rhombs were separated by rather broad areas, in which no pores were developed. The number of pore-casts in the separate rows could not be ascertained but seems to have been small.

The ambulacral area and the mouth remain unknown. The anus is a circular opening, 5.5 mm in diameter, probably being enclosed by 4 plates. It holds a high position, about 12 mm below the summit of the mould just where the back-line of the theca begins its vertical course.

Neither hydropore nor gonopore are visible, if originally present.

The base is somewhat damaged. So nothing can be stated about an eventual stem.

Remarks: — This species is well distinguishable from all other forms hitherto described. In general appearance it approaches to *Caryocystites* as pointed out, moreover, by JAEKEL (1899, p. 339). With regard to the location of the anus *Stichocystis alutacea* (as well as *S. geometrica*) agrees with *Heliocrinites*.

Regional distribution: — Sweden, Västergötland: Jonstorp. — Northern Germany [drift boulder (JAEKEL 1899), explanation of Pl. 8].

Stratigraphic range: — Probably Chasmops limestone, Upper Llandeilian.

## Superfamily **Caryocystitida** (JAEKEL 1918) n. nomen.

### Family **Caryocystitidae** (JAEKEL 1918) n. nomen.

This family contains an assemblage of forms, the interrelations of which must be said to be rather intricate. So it is no wonder that in previous literature different opinions have been advanced regarding the grouping of the species concerned, at the same time as there has been some confusion in the nomenclature. Further, the Caryocystitidae are connected closely with the Echinospaeritidae. In fact they have by several authors not been recognized as a separate family but taken with the Echinospaeritidae, as e.g. by BATHER and by JAEKEL in 1899.

The morphogenetic relations between the genera of the Caryocystitida remain rather obscure even after a study of the abundant Swedish material. For there is no difference in the stratigraphic appearance of their oldest representatives.

BATHER (1906, p. 14 seq.) presented an elucidatory survey of the Echinospaeritidae in a wider sense. Here i.a. he re-established the generic name *Heliocrinites* EICHWALD 1840, which had been suspended without any cause. The species belonging there had usually been referred to *Caryocystites* BUCH 1844. Now BATHER displayed the real application of the name last-mentioned, viz. for forms designated as *Amorphocystis* by JAEKEL. The present writer

agrees with BATHER in the conception of the generic names. Yet a slight modification of the diagnoses of the genera proved necessary.

In his revision of 1918 (p. 99) JAEKEL accepted the restoration of *Helio-crinites*. But he maintained both *Amorphocystis* and *Caryocystites*. As the names were not accompanied by any diagnoses we are unaware of the contents of the three genera in the sense of JAEKEL. As far as the present author can see, it might not be convenient to recognize more than two genera, namely *Caryocystites* and *Heliocrinites*, which thus correspond to *Amorphocystis* and *Caryocystites* respectively in JAEKEL 1899.

### Genus *Caryocystites* BUCH 1844.

**Genotype:** — *Caryocystites angelini* (HAECKEL 1896) [*C. testudinarius* "auctorum"].

**Synonyms:** — See BASSLER 1938 (p. 62). Addendum: *Sphaeronites* (ex parte) HISINGER 1837 b.

**Diagnosis:** — A genus of Caryocystitidae with elongated theca, its height being more than twice the greatest diameter; sculpture of the thecal plates not very prominent; canals connecting the pores generally compound; anus near (generally close above) the middle of the theca.

**Remarks:** — In his diagnosis of *Amorphocystis*, JAEKEL (1899, p. 338) stated i.a.: — "Mund im Scheitel schlitzförmig, anscheinend regelmässig, nur mit 2 Fingern an den Enden des Schlitzes versehen". That holds good of *Caryocystites angelini* but is not true of *C. lagenalis* n. sp., in which the mouth is triangular; there are 3 brachiole-facets in that species.

**Regional distribution:** — Sweden, Estonia (JAEKEL 1899, p. 339), ? N. America (BASSLER 1919, p. 133).

**Stratigraphic range:** — Middle Ordovician—lower part of Upper Ordovician (horizon of the Estonian species uncertain, according to JAEKEL l.c.).

### *Caryocystites angelini* (HAECKEL 1896).

Pl. 4, figs. 6—9.

1831 Description without name. — HISINGER, p. 106, Pl. 6, figs. a (sinistra), a (dextra) [figs. inverted], the fig. without legend placed between those mentioned.

1837 *Sphaeronites Citrus* rostris elongatis. — HISINGER 1837 b, p. 91, Pl. 25, fig. 9 d (dextra). (As pointed out by BATHER (1906, p. 16), this fig. is rightly 8 d, the stippled line having been inserted wrongly by the lithographer; in the explanation of the plate it stands, accordingly, as "*Sphaeron. testudinaria*", which is the legend of fig. 9). [Fig. inverted.]

1846 *Caryocystites testudinarius* HIS. — BUCH 1846 a, p. 107, Pl. 1, fig. 20.

1846 *Caryocystites testudinarius*, HISINGER. — BUCH 1846 c, p. 33, Pl. 3, fig. 5.



- 1876 *Sphaeronites testudinaria* HIS., Leth. Suec., t. XXV, fig. 9 d. — LINNARSSON 1876, p. 79 (9).  
 1878 *Caryocystis testudinaria* (HIS. ex parte) v. BUCH. — ANGELIN 1878 a, p. 29, Pl. 13, figs. 4—9.  
 1878 *Caryocystis dubia* ANG. — ANGELIN 1878 a, p. 29, Pl. 19, fig. 17 [fig. inverted].  
 1882 *Caryocystites testudinaria*. — TULLBERG 1882 a, p. 233 (16).  
 1888 *Caryocystis testudinaria* H. — LINDSTRÖM 1888 a, p. 16.  
 1891 *Caryocystis testudinaria*. — CARPENTER, p. 4.  
 1896 *Caryocystis Angelini*. — HAECKEL, p. 59, Pl. 2, fig. 27.  
 1899 *Amorphocystis Buchi* n. sp. — JAEKEL, p. 339, Pl. 9, fig. 8.  
 1900 *Caryocystis Angelini*. — BATHER, p. 55, text-fig. 17.  
 1906 *Caryocystis Angelini*. — BATHER, p. 16.  
 1934 *Amorphocystis buchi*. — GISLÉN, p. 2, text-fig. 1.

As mentioned above, the confusion regarding the specific name of *Caryocystites angelini* was caused by an error at lithographing Pl. 25 of HISINGER's 'Lethaea Svecica'. The case was cleared up by BATHER (1906, pp. 15—16), who stated that the valid specific name is *angelini*, proposed by HAECKEL (1896) "more by accident than design"! (BATHER 1906, p. 16).

It is likely that this species was alluded to in 1802 already by HISINGER (cf. p. 4 above).

**L e c t o t y p e:** — RM Ec 4207.

HAECKEL's description — as seems generally to have been the case for that author — was probably not based on the study of actual fossil material but on statements by earlier investigators. So a type-specimen has had to be selected. A specimen agreeing in detail with HAECKEL's figure (which is a coyp from BUCH) and, at the same time, well-preserved could not be procured. But among the polymorphous forms of this species, the specimen now designated as lectotype has tolerably the same shape. The oral pole is unfortunately a little damaged.

**T y p e l o c a l i t y:** — Böda Harbour, Öland.

**T y p e s t r a t u m:** — Lower Chasmops limestone, Middle Ordovician.

**M a t e r i a l:** — More than 200 specimens were available to the author; in general they are fragmentary, however. In the HISINGER collection there are 4 badly preserved specimens, none of which is the original of figures in HISINGER's papers. On the other hand the specimen RM Ec 4327 (Pl. 4, fig. 9 a) has a considerable resemblance to Pl. 7, figs. a-a, in HISINGER 1831. But there is no annotation to indicate that this specimen has belonged to the HISINGER collection. The same specimen shows also a certain similarity to the figure given by ANGELIN (1878 a, Pl. 13, fig. 4), but is hardly its original.

**D i a g n o s i s:** — A species of *Caryocystites* with a moderate number of thecal plates in the adult (about 60 in the lectotype); theca more or less tube-shaped with irregular swellings; the mouth an elongated slit with a

brachiole-facet at each end; stem feebly developed, thread-like, or quite lacking.

**Description of the lectotype:**—General shape of the theca. The theca is very long and narrow, being pinched in near to the base and in the height of the anus. This pinching in is best visible in lateral view. The median portion of the theca is less swelled up than in many other specimens.

**Measurements.** Height of the theca 80 mm; greatest diameter 27 mm.

**Thecal skeleton.** The theca is composed of fairly equal-shaped plates. Yet both almost quadrangular and heptagonal plates are found. The largest plates, many of them clearly elongated, are in the equatorial region, whereas the plates at the poles are somewhat minor. The plates are arranged in 10 tolerably regular circlets. The contents of plates in each circlet is indicated in the table below, in which the different circlets (not clearly defined) are denoted by Roman numerals, I corresponding to the lowest one. For comparison some other (smaller) specimens, in which the sutures are recognizable, have been included in the table:

|               | I | II | III | IV | V  | VI | VII | VIII | IX | X  | Approximate number of plates                     |
|---------------|---|----|-----|----|----|----|-----|------|----|----|--------------------------------------------------|
| RM Ec 4207 .. | 5 | 6  | 5   | 6  | 6  | 6  | 8   | 8    | 8  | 4? | 62                                               |
| RM Ec 4327 .. | 5 | 4? | 6   | 6  | 5  | 6  | 6   | 7?   |    |    | 45                                               |
| RM Ec 4467 .. | 5 | 6  | 4   | 6  | 5? |    |     |      |    |    | 26                                               |
| RM Ec 4242 .. | 5 | 6  | 6   | 6  |    |    |     |      |    |    | {Unknown, the upper portion of the theca wanting |

**Surface structures of stereom.** In some plates there is a marked umbo, from which low ridges radiate to the angles. The tangential canals of the pore-system are too fine to call forth a very conspicuous sculpture on the surface of the plates.

**Pores of the thecal plates.** The pores are not very abundant, but are connected by compound pore-canal, on account of which the number of tangential canals in a pore-rhomb is considerably greater than that of the pores. Thus in one pore-rhomb e.g. there are 11 pores in each half but 29 tangential canals. In this case each two pores are connected by two or three canals. Those are extended side by side and are very feeble. So, as pointed out by JAEKEL (1899, p. 338), the whole of the pore-rhomb is depressed into the stereothek.

**The ambulacral area,** as mentioned, is not well-preserved, but it was no doubt rectangular or trapezoidal, with a brachiole-facet at each end. — A hydropore is not visible.

**Alimentary canal.** The mouth has been an elongated slit.

The anus is a pentagonal opening lying somewhat above the middle of the theca, in the upper pinching in. The greatest diameter amounts to 6 mm. An anal pyramid is not preserved.

Just to the right of the line connecting the centres of mouth and anus there is a small cordate pore (greatest diameter 2 mm) at the base of the posterior brachiole-facet. This aperture may be interpreted as gonopore.<sup>29</sup>

The base of the theca is flattened in the lectotype. The initial portion of the stem is present as a feeble protuberance (diameter about 1 mm).

**Remarks on typoids:** — Complete specimens are very rare in the material available and are mainly found among small-sized individuals presumably representing immature growth-stages.

The general shape of the theca varies strongly in different specimens. A few forms are illustrated in Pl. 4. There are forms, however, in which the swellings of the body are still more pronounced. The location of these swellings is also exceedingly variable. Therefore the name *Amorphocystis* suggested by JAEKEL is very expressive and would have been very fitting if valid.

The measurements of some specimens: —

| (Measurements in mm)   | RM Ec 4206 | Spec. in SGU | RM Ec 4327 | RM Ec 4609 | RM Ec 4467 |
|------------------------|------------|--------------|------------|------------|------------|
| Height of the theca .. | 77         | 72           | 48         | 35.5       | 28         |
| Greatest diameter .... | 27.5       | 31           | 15         | 14         | 12.5       |

In details of the surface structures of the plates and the development of the pore-system all specimens seem to agree fairly well.

The mouth is invariably elongated with a brachiole-facet at each end. ANGELIN (1878 a, Pl. 13, fig. 5) indicated, besides the aperture interpreted as gonopore, a second opening somewhat above the former. ANGELIN's figure was reproduced by BATHER (1900, p. 55) and the opening was called madreporite. Such a pore could not be traced, however, in any specimen examined by the present writer. In RM Ec 4327 the gonopore is covered by a low pyramid of 3 valvals (Pl. 4, fig. 9 b, below; unfortunately details do not appear clearly from this fig.).

The anal opening seems to hold an approximately constant position.

**Discussion:** — As pointed out repeatedly above, this species is very polymorphous. Yet it is sufficiently well characterized by a number of features common to the different forms. Its nearest relative is *Caryocystites*

<sup>29</sup> The single aperture found in the Caryocystitida between the mouth and the anus was interpreted by JAEKEL (1899, p. 320), undoubtedly correctly, as gonopore: "Der Klap-penverschluss deutet auf einen gelegentlichen Austritt von Stoffen, würde aber mit einer dauernden aufsaugenden Funktion dieser Körperöffnung schwer in Einklang zu bringen sein."

*esthoniae* (JAEKEL), in which the thecal skeleton is composed of a great number of small plates. — The differences from *Caryocystites lagenalis* n. sp. will be mentioned in the description of that species.

Regional distribution: — Sweden, Öland: Böda Harbour, Dödevi, Frönäs, Lerkaka, Lopperstad bodar.<sup>30</sup>

Stratigraphic range: — Lower Chasmops limestone, Upper Llandeilian.

*Caryocystites lagenalis* n. sp.

Pl. 4, figs. 10—11. Pl. 5, fig. 1.

Derivation of name: — From Lat. *lagena*, bottle, with allusion to the shape of the theca.

Holotype: — UM ec 91.

Type locality: — Kullsberg, Dalarna.

Type stratum: — Green marl-shale belonging to the Kullsberg limestone, Middle and (basal) Upper Ordovician.

Material: — About 80 specimens [RM, UM], several of which are pretty well preserved, whereas others are fragmentary.

Diagnosis: — A species of *Caryocystites* with comparatively few thecal plates (in the holotype 42 only); theca more or less bottle-shaped tapering upwards and downwards from the swollen dorso-medial portion; mouth triangular; 3 brachiole-facets; stem relatively thick.

Description of the holotype: — General shape of the theca. The specimen is strongly compressed (secondarily), so that the anterior thecal wall is almost in contact with the posterior one. The theca is long but less tube-shaped than in *Caryocystites angelini*. It reaches its greatest width approximately at the upper limit of the lower third.

In the table below are given measurements and analysis of the theca in the holotype and, for comparison, in some other specimens, giving at the same time an idea of the construction of the thecal skeleton. The different circlets are denoted by Roman numerals, I indicating the lowest circlet. In many cases it is conditional whether a plate should be referred to one circlet or to an adjacent one, the plate in question being located between the two circlets.

It should be emphasized again that from this table one must not draw the conclusion that the thecal plates are disposed in regular circlets. On the

<sup>30</sup> It is questionable whether the specimens (in RM) were collected from solid rock at the two localities last mentioned, which lie considerably S of the known extension area of Lower Chasmops limestone in Öland.



|                                | Measurements<br>in mm  |                      | Number of plates in circlet |    |     |    |   |    |     |      | Number<br>of plates |
|--------------------------------|------------------------|----------------------|-----------------------------|----|-----|----|---|----|-----|------|---------------------|
|                                | Height of<br>the theca | Greatest<br>diameter | I                           | II | III | IV | V | VI | VII | VIII |                     |
| UM ec 99 .....                 | 88                     | 38                   | 5                           | 8  | 9   | 6  | 5 | 5  | 5   | 5    | 48                  |
| UM ec 89 <sup>f</sup> .....    | 87                     | 35                   | 5                           | 8  | 7   | 7  | 5 | 11 | 5   |      | 48                  |
| UM ec 91 (holo-<br>type) ..... | 85                     | —                    | 5                           | 8  | 7   | 7  | 5 | 5  | 5   |      | 42                  |
| UM ec 98 .....                 | 56                     | 21                   | 5                           | 9  | 9   | 9  | 5 | 8  | 5   |      | 50                  |
| RM Ec 1829 ...                 | 54                     | 17                   | 5                           | 8  | 6   | 7  | 7 | 7  | 5   |      | 45                  |

contrary, there are considerable anomalies in this respect. In the holotype the pavement of the anterior side is more regular than that of the posterior one.

**Surface structures of stereom.** Some plates, especially in the upper half of the theca, are provided with an umbo, from where low ridges originate to extend diagonally to the umbos of adjacent plates. As a rule only 4 ridges emanate from each umbo, the whole ornament acquiring the approximate shape of a St Andrews cross, the rays of which are arranged perpendicularly to the suture separating two plates. On account of the compressed state of the holotype, the surface structures are less prominent than in certain other specimens. As in the preceding species, the tangential pore-canals by themselves do not contribute to the ornament.

**Pores of the thecal plates.** The pores are not very well visible in specimens that are not abraded. They are not very numerous but are connected by systems of compound tangential canals. On the whole, the development of the pore-system can be said to agree with that of *Caryocystites angelini*. The number of pores in a rhomb stands of course in relation to the length of the suture crossed by the pore-canals.

The ambulacral area is not preserved in the holotype, since the very top is wanting.

**Alimentary canal.** The mouth, in consequence, is not visible. In other specimens it is seen to be triangular. The transverse section of the oesophagus, close below the mouth, exposed in the holotype, is nearly rectangular in outline. The anus is situated just above a line separating the upper half of the theca from the lower one. It is a large pentangular opening, the diameter of which is about 7 mm.

The gonopore is subcircular, having a diameter of about 3 mm. It lies almost in the same vertical plane as the anus, 9 mm below the oral pole.

The proximal portion of the stem is attached to the theca. In the length of 7 mm there are 7 columnals. The joints seem to be somewhat undulating. The diameter of the stem is 5.5 mm, a measurement which might have been increased a little, however, by the compression of the specimen.

**Remarks on typoids:** — In general shape the theca does not vary as much in different specimens as in the case of *Caryocystites angelini*. The relative width is generally smaller in young individuals than in the adult. In many specimens — even in young ones — the ornament of the thecal skeleton is decidedly more pronounced than in the holotype but it is of the same general character.

The structure of the pore-system is well recognizable in certain specimens which are somewhat abraded. In UM ec 98, e.g., 5 or more tangential pore-canals are seen to form a compound system connecting pores at each side of the suture.

The ambulacral area is well preserved in certain specimens, e.g. in UM ec 89. There are 3 brachiole-facets, one at each angle of the triangular mouth. In the specimen in Pl. 4, fig. 10, the anus is covered by a pyramid of 5 valvals. The position of the anus is rather constant, but may be a little higher or a little lower than in the holotype. No columnals are preserved otherwise than in the holotype.

**Discussion:** — *Caryocystites lagenalis* differs in several respects from the other Swedish species of the same genus: In general shape of the theca it is less polymorphous; the theca is composed of a minor number of plates; the surface ornament of the plates is more developed; there are 3 brachiole-facets instead of 2; the mouth is triangular and not an elongated slit; the gonopore is almost in the same vertical plane as the anus; the stem is considerably better developed. The species under consideration shows no very close affinity to any other form previously described.

**Regional distribution:** — Sweden, Dalarna: Kullsberg, Am-tjärn, Holn, Sättra (specimens labelled "Hosjön" might be also from this locality).

**Stratigraphic range:** — Kullsberg limestone, Upper Llandeilian—Lower and Middle Caradocian.

### *Caryocystites* sp.

In the SGU collection there is a piece of Chasmops limestone from the quarry at Lappgrubban, Lockne, Jämtland (coll. P. THORSLUND), containing a badly preserved theca. From its elongated shape it can safely be inferred that it belongs to *Caryocystites*, but a closer determination is rendered impossible by the poor state of preservation. Among known species it has undoubtedly to be compared in the first hand with *Caryocystites lagenalis* n. sp.

Another fragment [SGU] from the same area and horizon is possibly conspecific with the specimen from Lappgrubban.

Genus *Heliocrinites* EICHWALD 1840.

Genotype: — *Echinospaerites balticus* EICHWALD 1829.

Synonyms: — See BASSLER 1928 (p. 109) and JAEKEL 1899 (p. 327, sub *Caryocystites*).<sup>31</sup>

Diagnosis: — A genus of Caryocystitidae with rounded, oval, or elongated theca, its height not (or inconsiderably) exceeding twice the greatest diameter; pores connected by simple tangential canals; anus generally within the upper third (in any case within the upper half) of the theca.

Regional distribution: — Sweden, Norway (EICHWALD 1845, p. 104; KJERULF 1865, p. 4; KLÆR 1901, p. 11: "*Echinospaerites* cf. *balticus* EICHW."), Britain (BATHER 1913, p. 494, § 559), France (KOENEN 1886, p. 248, sub *Caryocystites*), Belgium (BATHER l.c.), Portugal (JAEKEL 1899, p. 330), Bohemia [besides the dubious "*Orocystites*", *Heliocrinites confortatus* (BARRANDE)],<sup>32</sup> Germany (FREYBERG 1923, p. 263 seq.), Estonia, USSR, Burma (BATHER 1906, p. 19 seq.; REED 1936, p. 10), China (REED 1917, p. 16 seq.; SUN 1936, p. 482; YIN & LU 1936—37).

Stratigraphic range: — Middle—Upper Ordovician or Lower Silurian. All extra-Swedish species hitherto described seem to be Middle Ordovician.

*Heliocrinites angustiporus* n. sp.

Pl. 5, fig. 2.

Derivation of name: — From Lat. *angustus*, narrow, with regard to the thin tangential pore-canals.

Holotype: — RM Ec 2445, a somewhat defective specimen.

Type locality: — Fjäckå, Dalarna.

Type stratum: — Chasmops limestone, Middle Ordovician.

Material: — Besides the holotype 6 specimens are available, all of them more or less imperfect.

<sup>31</sup> *Orocystites* BARRANDE 1887 was taken as a synonym of *Heliocrinites* by JAEKEL 1899, BATHER 1906, HECKER 1923, and ZITTEL-BROILI 1924. BASSLER (1938, p. 142), following BATHER 1900, ranked it as a separate genus. "The peculiar elevation of the anus on an incipient anal tube, while distinguishing this species from all others of the genus [*Heliocrinites*], is perhaps not enough to warrant the retention of BARRANDE's *Orocystis*" (BATHER 1906, p. 18). BATHER (l.c.) stated that *Heliocrinites* ("*Orocystites*") *helmhackeri* v. *thuringiae* (Jaekel) might be a distinct species. FREYBERG (1923, p. 264), on the other hand, identified it with *H. helmhackeri*.

<sup>32</sup> JAEKEL (1899, p. 330) regarded "*Echinospaerites*" *confortatus*, *E. vexatus*, and *E. quaerendus*, all of BARRANDE 1887, as synonymous. According to FREYBERG (1923, pp. 248, 263), the last-mentioned is a distinct species belonging to *Echinospaerites*. No opinion was uttered of *E. vexatus*.

**Diagnosis:** — A species of *Heliocrinites* with largely globular theca; number of thecal plates in the holotype 150—170, according to approximative estimate; thecal plates varying in shape and size; number of pores 12—15 in the larger plates, fewer in the minor ones; tangential pore-canal thin, spaced from each other.

**Description:** — **General shape of the theca.** The theca is tolerably globular, as appears from the following measurements.

| (Measurements in mm)        | RM Ec 2445<br>(holotype) | RM Ec 2463 | Specimen<br>in SGU |
|-----------------------------|--------------------------|------------|--------------------|
| Height of the theca .....   | 33.5                     | about 30   | 42.5               |
| Diameter of the theca ..... | 32                       | » 30       | 45.5               |

**Theca skeleton.** The sutures between the plates are very obscure. The size and shape of the single plates must, therefore, be inferred as a rule from the ornament. Small plates are intercalated between the medium-sized and large ones, as in *Echinospaerites*. A considerable portion of the test is preserved in the holotype only, but also in this specimen a good deal of the theca is wanting. By counting the plates on a half of the theca, their total number could be estimated at 150—170.

**Surface structures of stereom.** The tangential pore-canal make a conspicuous ornament of ridges dilating from centre to centre. These ridges are thin and low and widely spaced from each other on account of the relatively sparse occurrence of pores, calling forth a certain similarity to *Stichocystis geometrica*.

**Pores of the thecal plates.** In the larger plates there are 12—15 pores, connected by the tangential pore-canal with pores of adjacent plates. The pores seem often to be arranged in such a way that about half the number opens around the centre of the plate and the others nearer to the periphery. By this means longer pore-canal come to alternate with shorter ones.

**The ambulacral area** is well elevated over the surface of the theca. It is not well preserved in any specimen but might have had 3 brachiole-facets in the holotype.

The shape of the mouth cannot be recognized. The anus, which lies just within the upper third of the theca, is covered by a high pyramid of 5 valvulae.

A little to the right of the line connecting the anus with the oral pole lies a small rounded gonopore. It is somewhat closer to the mouth than to the anus.



The base is not preserved in any specimen available. So it cannot be stated whether a stem has been developed or not.

**Discussion:** — This species seems to be well defined by the character of the pore-canals. Further it may be observed that the number of thecal plates is greater than in most other species of *Heliocrinites*.

The Swedish form has some resemblance to the East Baltic *Heliocrinites balticus* EICHWALD from about equivalent strata (stage C<sub>2</sub>). But in this species the tangential pore-canals are decidedly higher and often somewhat fusiform. The theca might be oval rather than globular.

*Heliocrinites confortatus* BARRANDE also displays some resemblance (stage d 4 of Bohemia; Thuringia). In this species the pore-ridges leave the umbos smooth, which is the case in our species too — at least in certain instances. According to BATHER (1906, p. 19) this feature is unfamiliar to other members of the genus. *Heliocrinites confortatus* differs from the Swedish form i.a. by the great number of pore-canals.

**Regional distribution:** — Sweden, Dalarna: Fjäckå, Vikarbyn [RM], Gulleråsen (boulder) [SGU]. — Östergötland: Norra Freberga [RM].

**Stratigraphic range:** — Chasmops limestone, Upper Llandoveryan.

### *Heliocrinites granatum* (WAHLENBERG 1821).

Pl. 1, fig. 1. Pl. 5, figs. 3—11.

- 1802 “— nytt species deraf” [*Echini genus*]. — HISINGER, p. 189, Pl. 7, fig. b.
- 1821 *Echinospaerites Granatum*. — WAHLENBERG, p. 53.
- 1828 *Sphaeronites granatum*. — HISINGER, p. 197, Pl. 5, fig. 1.
- 1837 *Sphaeronites granatum* (*Sphaer. testudinaria*). — HISINGER 1837 a, p. 115, Pl. 8, fig. 1.
- 1837 *Sphaeronites testudinarius*. — HISINGER 1837 b, p. 92, Pl. 25, figs. 9 a—d [non fig. d dextra (= *Caryocystites angelini* (HAECKEL); cf. the list of synonyms for this species above)].
- 1840 *Sphaeronites Granatum*. — BUCH, p. 58.
- 1841 *Sphaeronites testudinaria* H. — [HISINGER] 1841 b, p. 62.
- 1842 *Sphaeronites testudinarius* oder *Granatum* HIS. — VOLBORTH 1842, columns 299, 302, Pl. 1, figs. 1—3.
- 1846 *Caryocystites Granatum* WAHL. — BUCH 1846 a, p. 105, Pl. 1, figs. 8—10, Pl. 2, fig. 4.
- 1846 *Caryocystites granatum*, WAHLENBERG. — BUCH 1846 c, p. 32, Pl. 3, fig. 4, Pl. 4, fig. 2.
- 1878 *Caryocystis granatum* WAHLENBERG. — ANGELIN 1878 a, p. 29, Pl. 12, figs. 27—29, ? Pl. 13, figs. 14—16, Pl. 14, figs. 22—23, 25, 27—28, ? 24, 26.
- 1888 *Caryocystis granatum* WBG. — LINDSTRÖM 1888 a, p. 16.
- 1891 *Caryocystis granatum*. — CARPENTER 1891, p. 4.
- 1896 *Heliocystis* (*Heliocrinum*) *granatum* L. BUCH. — HAECKEL, p. 58.

1899 *Caryocystites granatum* WAHLENBERG sp. — JAEKEL, p. 329, Pl. 9, fig. 2.

1906 *Heliocrinus granatum* (WAHLENB.). — BATHER, p. 17.

[Non *Echinospaerites Granatum* SCHLOTHEIM 1826, column 311, figs. 1 a—c (= *Echinoencrinites senckenbergii* MEYER). — Non *Caryocystites granatum*. FORBES 1848, p. 512, Pl. 21, fig. 4 (= *Heliocrinites balticus* EICHWALD ?, fide JAEKEL 1899, p. 330; BATHER 1906, p. 17). — Non *Caryocystites granatum* MCCOY 1851, p. 62; as the preceding.]

A number of quotations of the species in text-books, faunal lists, &c., were not considered at compiling the list of synonyms.

**Lectotype:** — UM ec 1857, a considerably worn specimen.

**Remarks:** — WAHLENBERG's description (1821) of "*Echinospaerites*" *granatum* was not accompanied by any figure. Therefore we have to designate a lectotype from the material upon which the original description was admittedly based. The WAHLENBERG collection in UM contains two specimens likely answering to this claim, for they have labels in the handwriting of WAHLENBERG. These are UM ec 1857 (Böda Harbour, Öland, the specimen having been procured by HISINGER) and UM ec 1859 (Vikarbyn, Dalarna). Unfortunately both are in a considerably poor state of preservation. Yet one of them has to be taken as lectotype, and we choose the Öland specimen. But the lectotype thus designated may be regarded as provisional, for there might be a chance that better specimens from the WAHLENBERG collection will be discovered in UM.

**Type locality:** — Böda Harbour, Öland.

**Type stratum:** — Lower Chasmops limestone, Middle Ordovician.

**Material:** — A large number of specimens were available to the writer, estimated at about 700. Good specimens are sparse, however. The HISINGER collection [RM] contains 7 specimens, but none of these can be supposed to represent specimens figured in HISINGER's papers. Of the specimens figured by ANGELIN (1878 a), only that represented in figs. 27—29 on Pl. 12 can be identified.

**Diagnosis:** — A species of *Heliocrinites* with oval or spheroidal theca, regularly of small size; the number of plates moderate (in the adult about 30—35); the number of pores about 30 in medium-sized plates; tangential pore-canals clearly separated from each other and defined sharply.

**Description:** — **General shape of the theca.** In the lectotype — as in most medium-sized and large specimens — the theca is oval, whereas small specimens are more spheroidal. Occasionally larger specimens also are spheroidal.

The following **measurements** should give an idea of the general habit of the theca. Where possible to make out, the approximate number of thecal plates is also given in the table.

| (Measurements in mm)          | 1<br>RM Ec<br>4304 | 2<br>RM Ec<br>3379 | 3<br>RM Ec<br>4197 | 4<br>UM ec 1857<br>lectotype | 5<br>RM Ec<br>3361 | 6<br>UM ec 5 | 7<br>RM Ec<br>3357 |
|-------------------------------|--------------------|--------------------|--------------------|------------------------------|--------------------|--------------|--------------------|
| Height of the theca . . . . . | 40                 | 30                 | 28                 | 27                           | 22                 | 20           | 19.3               |
| Greatest diameter . . . . .   | 30                 | 24                 | 22.5               | 20                           | 18                 | 16           | 16.6               |
| Number of thecal plates..     | —                  | 32                 | 35                 | —                            | 35                 | 30           | 34                 |

| (Measurements in mm)          | 8<br>RM Ec<br>4473 | 9<br>RM Ec<br>4853 | 10<br>RM Ec<br>4474 | 11<br>RM Ec<br>4475 | 12<br>RM Ec<br>4476 | 13<br>RM Ec<br>4477 | 14<br>RM Ec<br>4478 |
|-------------------------------|--------------------|--------------------|---------------------|---------------------|---------------------|---------------------|---------------------|
| Height of the theca . . . . . | 19                 | 14                 | 12.7                | 12.4                | 12                  | 9                   | 7                   |
| Greatest diameter . . . . .   | 13.7               | 13                 | 11.8                | 12.8                | 13                  | 8.7                 | 6.5                 |
| Number of thecal plates..     | —                  | 30                 | 31                  | 25                  | 27                  | 20                  | 21                  |

The specimens measured originate from the following localities: Böda Harbour, Öland (1, 3—4, 8, 10—14); Lopperstad, Öland (9); N. Freberga, Östergötland (2, 5, 7); Amtjärn, Dalarna (6).

The specimen in column 1 of the above table is an exceptionally large one. Yet single specimens reached still greater dimensions. Thus the largest specimen available [RM Ec 4880, from Öland] has a height of 57 mm. Unfortunately the state of preservation does not admit of a thorough examination. Numerically the strongest representation has the size-order 20—30 mm.

**Thecal skeleton.** The thecal plates are arranged largely in circlets, which are not regular, however, but vary in number of plates. The construction of the theca may be demonstrated by a few examples. The circlets are denoted by Roman numerals, I corresponding to the lowest one.

|                      | I | II | III | IV | V | VI | Approximate<br>number of<br>plates |
|----------------------|---|----|-----|----|---|----|------------------------------------|
| RM Ec 4197 . . . . . | 4 | 8  | 8   | 7  | 5 | ?  | 32                                 |
| RM Ec 3361 . . . . . | 4 | 6  | 8   | 8  | 5 | 4? | 35                                 |
| RM Ec 4853 . . . . . | 4 | 9  | 8   | 6  | ? |    | 27                                 |
| RM Ec 4478 . . . . . | 4 | 6  | 6   | 5? |   |    | 21                                 |

The dimensions of the specimens here mentioned appear from the table of measurements above. Further it should be pointed out that the referring of certain plates to the one circlet or the other is conditional.

The plates of the basal circlet seem to be regularly 4 in number. But in most specimens they are so intimately connected that the individual plates cannot be recognized. In RM Ec 4853, where they are especially clearly

visible, 3 of the basal plates are seen to be wedge-shaped, whereas the fourth — the anterior one — is broadly pentagonal.

The plates of the lateral circlets are as a rule remarkably equal in size and shape, most of them being hexagonal or pentagonal in outline. In the small specimen just referred to they have a diameter of about 5 mm, in a medium-sized specimen [RM Ec 3361] the average diameter is about 7 mm and amounts to about 11 mm in extreme instances [RM Ec 4304].

**Surface structures of stereom.** The tangential pore-canals are relatively broad and are sharply defined. Where not strongly affected by weathering, they reach a considerable height, so that a transverse section through a pore-rhomb presents a comb-like appearance (Pl. 5, fig. 3). In typical forms the rhombs are composed of 3—7 ridges. There are no broad interspaces between the different rhombs.

**Pores of the thecal plates.** The average number of pores in a thecal plate is 30 but is of course dependent on the size and shape of the plate. The pores are disposed along the radii running to the angles of the plate.

It was already mentioned above (p. 52) that the pores with short tangential canals in immature specimens have a certain resemblance to diplopores.

**The ambulacral area and the skeleton elements surrounding the gonopore** form a small eminence, wedge-shaped or elongated pentagonal in outline. JAEKEL (1899, p. 328) proposed 3 brachiole-facets to be present. Undoubtedly this is true partially, but a great many specimens have 2 brachiole-facets only. Thus, as in *Echinospaerites*, the number of brachiole-facets (and of course of brachioles) is subject to a certain variation. But we can confirm JAEKEL's suggestions (l.c.) that figs. 26 and 27 on ANGELIN's Pl. 14 are mere constructions, and that it seems questionable whether fig. 26 really applies to *Heliocrinites granatum* (cf. below).

**Alimentary canal.** The mouth — according to the shape of the ambulacral area — is either rounded—triangular, or somewhat elongated. The anus is a round or pentagonal opening behind the mouth, being separated from it by a space corresponding approximately to the diameter of the lateral plates in the specimen in question. A high anal pyramid of 5 valvulae was ascertained in one specimen only [RM Ec 3368]. The anus is wider than the mouth.

The gonopore, which is a small rounded aperture, lies close to the mouth, as just mentioned. It is somewhat to the right of a line connecting the centres of mouth and anus.

The base of the theca shows a point of attachment for a very thin stem. No columnals have been observed, however.



**Discussion:** — The description here given is based on material from Öland, Dalarna, and Östergötland. In the collections from the last-mentioned province there is, however, a large number of specimens, which agree essentially with typical representatives of *Heliocrinites granatum* but show some difference in certain respects. The rhomb-ridges are namely finer and are more numerous, which is true, in consequence, of the pores also. In most cases the rhombs give the impression of being flatter than in the typical form. But this feature may be conditioned by secondary alterations. The present writer is not inclined to regard these characters as constitutive for a separate species, all the more as transition forms lead imperceptibly from one type to the other. Therefore it is impossible to produce a satisfactory diagnosis and on that account it would be useless to propose even a subspecific name. In order not to conceal the paratypical character of the forms concerned, it would be suitable, however, to refer to them as "*Heliocrinites granatum* f." Further it should be noted that the extremes of such aberrant types approach to *Heliocrinites ovalis* (ANGELIN). — By earlier authors (TÖRNQUIST 1875, p. 66; TULLBERG 1882 b, p. 25; JÖNSSON 1887, p. 19) the *granatum*-forms from Östergötland have been denoted simply as "*Caryocystites granatum*".

As appears from the list of synonyms above, certain figures communicated by ANGELIN and claimed to represent *Heliocrinites granatum*, cannot be referred to this species without reserve. The originals of the figures could unfortunately not be identified and, therefore, their belonging cannot be decided. The theca figured in ANGELIN's Pl. 13, figs. 14—15, displays an unusually irregular pavement, and, moreover, is pentangular in oral as well as in lateral view. Figs. 24 and 26 in Pl. 14 represent specimens, in which the number of thecal plates is obviously larger than in the typical form.

Of species described from foreign areas, *Heliocrinites qualus* (BATHER 1906) and *H. fiscella* (BATHER 1906) seem to be the only ones showing some similarity to the Swedish form. Both species mentioned are from the Naunkangyi beds (equivalent to the so-called Echinospaerites limestone, Lower and Middle Llandeilian, of the East Baltic provinces, according to REED 1906, p. 85) in Burma. *H. qualus* was said by BATHER (1906, p. 24) to agree with the Swedish species in the distinctness of its rhomb-ridges, whereas shape and size of the thecae are very different. In *H. fiscella*, on the other hand, the theca seems to be constructed very much in the same way as in *H. granatum*, but the thecal plates were described as "axially folded, and bearing a few very prominent ridges" (BATHER 1906, p. 21).

**Regional distribution:** — Sweden, Öland: Böda Harbour, Dödevi, Lopperstad bodar (boulder?; cf. p. 116, foot-note 30). — Östergötland: N Freberga, Karstorp. — Dalarna: Amtjärn, Boda, Fjäckä, Furudal, Klittberg, Kårgårde, Orsbleck, Skattungbyn, Sollerön, Vikarbyn, Åberga,

Östbjörka (all localities mentioned verified by museum specimens), Gulleråsen, Nittsjö (TÖRNQUIST 1874, p. 14). — Jämtland: contained in boulders at several localities (WIMAN 1894, p. 268; 1897, p. 273; 1900, p. 139; MOBERG 1911, p. 148). — Scania: Tommarp, Tosterup (FUNKQUIST 1919, p. 38; the present writer did not succeed in finding the specimens in the collections in LM). — ? Siberia (specimens in drift-ice E of Greenland were supposed to originate from the northern coast of Siberia, if not brought to Greenland with stones used as ballast; JAECKEL 1899, pp. 153—154, 329).

A "*Heliocrinus* cf. *granatus*" was mentioned by REED (1936, p. 10) from the southern Shan States. Since the form in question was said to recall *Caryocystites granatum* of FORBES (1848), however, it might have no connexion with *Heliocrinites granatum* (WAHLENBERG).

Stratigraphic range: — Lower Chasmops limestone, Upper Llandeilian.

### *Heliocrinites ovalis* (ANGELIN 1878).

Pl. 6, figs. 7—10.

- 1878 *Caryocystis ovalis* ANG. — ANGELIN 1878 a, p. 29, Pl. 27, figs. 11 (two figs. have this designation: — one showing the holotype in posterior view, the other the same in basal view; as to the last-mentioned, an "a" was evidently omitted by the lithographer), 11 b.
- 1878 *Caryocystis tenuistriata* ANG. — ANGELIN 1878 a, p. 29, Pl. 12, figs. 25—26.
- 1888 *Caryocystis ovalis* A. — LINDSTRÖM 1888 a, p. 16.
- 1888 *Caryocystis tenuistriata* A. — LINDSTRÖM 1888 a, p. 16.
- 1896 *Heliocystis ovalis* ANGELIN. — HAECKEL, p. 59.
- 1896 *Heliocystis tenuistriata* ANGELIN. — HAECKEL, p. 59, Pl. 2, figs. 25—26 (cop. from ANGELIN 1878 a).
- 1917 *Caryocystis ovalis* ANG. — REED, p. 17.
- 1917 *Caryocystis tenuistriata* ANG. — REED, p. 17.

Holotype: — RM Ec 2782, largely exfoliated, with imperfect actinal region.

Type locality: — Jonstorp (Mösseberg), Västergötland.

Type stratum: — Chasmops limestone, Middle Ordovician.

Material: — Some 60 specimens, many of them unsatisfactorily preserved.

Diagnosis: — A species of *Heliocrinites* with ovoid theca (in some specimens spheroidal), somewhat compressed in sagittal direction so that the theca is oval in transverse section; thecal plates about 40 in number, disposed in 5—6 irregular circlets; pore-rhombs of fine densely set tangential canals; peristome well projecting; probably 3 brachiole-facets; periproct slightly projecting, situated approximately 90 degrees in solar direction of the gonopore (but in a lower plane); gonopore at the base of the peristomal projection; a faint stem has been present.

**Description of the holotype:**—General shape of the theca. The theca is ovoid, compressed in sagittal direction. When seen in anterior or posterior view its width is but slightly minor than the height, whereas the theca is decidedly oval when observed from one of the sides. The peristomal projection is broken off near its base.

**Measurements.** Height (excluding the peristomal projection) 39 mm; greatest diameter 34.5 mm; diameter perpendicularly to that mentioned, 29 mm.

**Thecal skeleton.** The base of the theca is probably pentamerous (represented as tetramerous in ANGELIN 1878 a, Pl. 27, fig. 11 dextra). The rest of the theca is formed by 4 or 5 irregular circlets, the plates of which are frequently interlocking owing to differences in size. In general the plates are large, however. Their total number seems to be approximately 36. Most plates are hexagonal.

**Surface structures of stereom.** Several plates (especially in the equatorial zone) have a clearly raised umbo but many are flattened or gently convex. In the actual specimen the surface structures are decidedly less pronounced than indicated in ANGELIN's fig. 11 sinistra, even though broad axial ridges crossing the sutures at right angles are visible in some plates.

**Pores of the thecal plates.** The pore-rhombs are composed of fine, densely set tangential canals, the number of which is about 16 in a space of 5 mm. There are hardly any interspaces between the different pore-rhombs. The number of pores in the single plates is of course conditioned by the size of the plates.

**The ambulacral area and the mouth** are not preserved. The transverse section of the peristomal projection close above its base is subpentagonal.

**The anus** is slightly protruding, its centre being in a plane about 5 mm below the base of the peristomal projection. The anus opens about 90 degrees in solar direction of the gonopore. Its outline is obscure, but seems to have been oval, with a long diameter of about 7 mm.

**The gonopore** (diameter about 2 mm) lies at the base of the peristomal projection.

**The stem** is not preserved. The cicatrix is roughly pentagonal, with a diameter of about 4 mm.

**Remarks on typoids:**—Like certain other species of *Helio-crinites*, this one is rather polymorphous. The following table gives an idea of the variations in shape of the theca. For the sake of comparison, the measurements of the holotype are repeated. The peristomal projection is excluded from the figures of the height. RM Ec 2784 is the type specimen of ANGELIN's "*Caryocystis tenuistriata*".

| (Measurements in mm)                               | RM Ec<br>2763 | RM Ec 2782<br>(holotype) | RM Ec<br>3324 | RM Ec<br>2784 | RM Ec<br>3325 | RM Ec<br>3156 |
|----------------------------------------------------|---------------|--------------------------|---------------|---------------|---------------|---------------|
| a. Height of the theca .....                       | 48            | 39                       | 35.5          | 33            | 30.5          | 24            |
| b. Greatest diameter .....                         | 39            | 34.5                     | 30            | 27.5          | 28.5          | 21.5          |
| c. Diam. perpendicularly to the<br>preceding ..... | 35            | 29                       | 28.5          | 22            | 25.5          | 19.3          |
| a : b-ratio .....                                  | 1.23          | 1.13                     | 1.18          | 1.20          | 1.07          | 1.12          |
| b : c-ratio .....                                  | 1.11          | 1.19                     | 1.05          | 1.24          | 1.12          | 1.12          |

As far as the writer is aware, the variations in shape are independent of any expressed tendency.

In certain specimens, e.g. in RM Ec 2784 just referred to, the sculpture of the thecal plates is less prominent than in the holotype, where it is indeed moderate too, however.

The development of the pore-rhombs and the number of tangential canals in the unit of measure are not subject to great variation in different specimens.

The peristomal projection is fairly well preserved in a few specimens (see Pl. 6, figs. 9—10 a). One gets no clear idea, however, of the shape of the ambulacral area. Probably it has been triangular with 3 brachiole-facets.

In cases where anus, gonopore, and stem are recognizable, they agree essentially in position and shape with corresponding organs in the holotype.

**Discussion:** — As appears from the list of synonyms above, this species, in the author's opinion, comprises also ANGELIN's "*Caryocystis tenuistriata*", from the same horizon and locality as the holotype of *Heliocrinites ovalis*. According to the description of ANGELIN (1878 a, p. 29), they would differ in the surface structure of the thecal skeleton and in different development of the peristome (*H. ovalis*: — well-marked umbos, no peristomal projection, "*C. tenuistriata*": — plates hardly umbonated, peristomal projection present). On comparison of the type-specimens we find that the theca of the last-mentioned form is fairly evenly rounded, being somewhat angular in *Heliocrinites ovalis*. The difference is not very great, however. As to the other distinguishing character proposed by ANGELIN, it has no significance, for, as mentioned, the actinal region of the holotype *Heliocrinites ovalis* is damaged. Yet it can be inferred from the remaining portion that a peristomal projection has been present, although broken off near to its base. At the investigation of the fossil-material available, the author found it impossible to draw a boundary between the two species proposed by ANGELIN. "*Caryocystis tenuistriata*" falls no doubt within the sphere of variation of *Heliocrinites ovalis*.

The present species is well distinguished from *Heliocrinites granatum* in typical development, i.e. by greater size of the theca, greater number of



thecal plates, fine and crowded tangential canals in the pore-rhombs, and by projecting peristome. But it was mentioned above (p. 125) that aberrant types of *Heliocrinites granatum* may approach to certain forms of *Heliocrinites ovalis*.

*Heliocrinites subovalis* (REED), from Shih-tien, Yunnan, in beds suggested to be equivalent to the Chasmops limestone, was said by REED (1917, p. 17) to display a certain affinity to "*Caryocystis tenuistriata*" and "*C. ovalis*". According to the description communicated by REED, the height-width index of the theca is considerably greater (1.8) in the Yunnan form, and the theca is composed of a much greater number of plates (60—70). The reason why REED (l.c.) proposed *Heliocrinites ovalis* to be devoid of a stem is obscure.

*Heliocrinites araneus* (SCHLOTHEIM) has some resemblance but differs i.a. in having a much greater number of thecal plates.

**Regional distribution:** — Sweden, Västergötland: Jonstorp (Mösseberg), Älleberg. — Östergötland: Fyrsten, N. Freberga. — Öland: Bocketorp (boulders). — ? Dalarna: Amtjärn.

**Stratigraphic range:** — Chasmops limestone, Upper Llandeilian.

### *Heliocrinites guttaeformis* n. sp.

Pl. 6, fig. 12.

**Derivation of name:** — From Lat. *gutta*, drop, alluding to the shape of the theca.

**Holotype:** — RM Ec 4021, an almost exfoliated specimen.

**Type locality:** — N. Freberga, Östergötland.

**Type stratum:** — Chasmops limestone, Middle Ordovician.

**Material:** — Besides the holotype, one specimen only is safely referable to this species. Further, there is a number of specimens which recall it but whose state of preservation does not admit of a definite determination.

**Diagnosis:** — A species of *Heliocrinites*, in which the height of the theca is  $1\frac{1}{2}$  of the greatest diameter; greatest diameter approximately in the equatorial plane; theca slightly compressed in transverse direction, tapering downwards to form a pointed base; number of thecal plates about 35, many of them with a well-marked umbo; pores connected by compound tangential canals, which are very fine, densely set in the pore-rhombs; pore-rhombs separated from each other by very narrow smooth zones; mouth an elongated slit obliquely to the sagittal plane, not projecting very much; anus at, or slightly below, the limit for the upper third of the theca, situated in a vertical plane slightly to the left of the gonopore; gonopore a little below the base of the posterior brachiole-facet; stem thread-like.

**Description:** — As indicated by the specific name, the general shape of the theca may be described as (reversed) guttiform. The theca looks widest in lateral view, owing to compression from the sides.

| (Measurements in mm)                               | RM Ec 4021<br>(holotype) | RM Ec 4039 |
|----------------------------------------------------|--------------------------|------------|
| a. Height of the theca .....                       | 37                       | 28.4       |
| b. Greatest diameter .....                         | 24.5                     | 19         |
| c. Diam. perpendicularly to<br>the preceding ..... | 20.5                     | 15.5       |
| a : b-ratio .....                                  | 1.50                     | 1.49       |
| b : c-ratio .....                                  | 1.20                     | 1.23       |

**Thecal skeleton.** The sutures between the thecal plates are generally not visible in either of the two specimens. The arrangement of the plates, therefore, could not be made out clearly. The number of thecal plates in the holotype could be estimated at about 35 by counting the umbos, which are as a rule well defined.

**Surface structures of stereom,** irrespective of the umbos, are obscure on account of the worn state of the thecae. In several cases the pore-rhombs might have been rather vaulted, however, owing to axial structures in the plates.

**Pores of the thecal plates.** As far as recognizable, the pores, at least in several instances, are connected by compound tangential canals. These are very fine and are densely set, so that there are about 5 of them in the space of 1 mm. The different pore-rhombs are separated from each other by narrow smooth zones.

**The ambulacral area** is elongated obliquely to the sagittal plane. Two brachiole-facets, of the same shape as in *Caryocystites angelini*, are present.

**Alimentary canal.** The mouth, in consequence of the shape of the ambulacral area, is an elongated slit. The anus is large (diameter 4.5 mm in the holotype), pentagonal. No covering plates are preserved. The anus opens in a vertical plane slightly to the left of the gonopore.

The gonopore is oval (long diameter 2 mm in the holotype). Its edge is 1 mm from the posterior side of the posterior brachiole-facet.

**Discussion:** — By the tapering basal portion and the broad middle and upper parts of the theca this species is well characterized among known forms of *Heliocrinites*. In the number of plates it is comparable with *H. granatum* and *H. ovalis*. In interrelations between anus and gonopore it approaches to the first-mentioned but differs i. a. in the position of the anus. — No foreign species displays a very great affinity to our form, as far as the writer is aware.

Regional distribution: — Östergötland: N. Freberga. — ? Öland: Kårehamn [Alböke (certainly boulder)].

Stratigraphic range: — Chasmops limestone, Upper Llandoilian.

*Heliocrinites prominens* (ANGELIN 1878)?

1878 *Caryocystis prominens* ANG. — ANGELIN 1878 a, p. 29, Pl. 12, figs. 18—21; Pl. 27, fig. 12; Pl. 28, fig. 11.

1888 *Caryocystis prominens* A. — LINDSTRÖM 1888 a, p. 16.

1896 *Heliocystis prominens* ANGELIN. — HAECKEL, p. 58.

1899 *Caryocystites aranea* v. SCHLOTHEIM sp. (ex parte). — JAEKEL, p. 330.

1906 *Heliocrinus aranea* (SCHLOT. 1826) (ex parte). — BATHER, p. 17.

?1907 *Caryocystites* sp. — WIMAN 1907 a, p. 121, Pl. 7, figs. 34—35.

Holotype: — Not recognized.

Type locality: — Not known ("Dalecarlia", ANGELIN 1878 a, p. 29).

Type stratum: — Not known.

Material: — Two badly preserved specimens seem to be referable to this species.

Diagnosis (ANGELIN's description, translated): — "Theca globular, slightly compressed; mouth narrow, elongated, with elevated margins; anal region moderately protruding; anus covered with 6 valvulae; plates umbonated, with fine tangential pore-canal."

The following measurements were given: — Height 33 mm; diameters 32 mm and 27 mm (ANGELIN 1878 a, p. 29).

Discussion: — Since the type-specimen seems to have been lost, the writer can give no definite opinion of the taxonomic status of *Heliocrinites prominens*. JAEKEL (1899, p. 330) suggested that it is synonymous with *Heliocrinites araneus* (SCHLOTHEIM), which was repeated by BATHER (1906, p. 17). As far as can be inferred from a comparison between ANGELIN's figures and figures of *Heliocrinites araneus*, an affinity is likely, but whether so great as to make the two forms identical can hardly be decided otherwise than by examining fossil material. For we must not suppose that the figures delivered by ANGELIN are quite adequate, and as to SCHLOTHEIM's figure a reserve is still more needed. There is, in fact, no very great similarity between the original figure (SCHLOTHEIM 1826, Pl. 1, fig. 3) and figures communicated by later authors [VERNEUIL 1845, Pl. 1, fig. 8 ("*Echinospaerites aurantium*"). EICHWALD 1860, Pl. 32, figs. 16—17 ("*Heliocrinus radiatus*"). JAEKEL 1899, Pl. 9, fig. 1. HECKER 1923, Pl. 2, fig. 6]. On the whole, the present writer is inclined to assume that the similarity between *Heliocrinites prominens* and *Heliocrinites aranea* refers to the development

of the pore-system and surface-structure of the thecal plates rather than to the general shape of the theca and the number of plates. According to VERNEUIL (1845, p. 20), the number of thecal plates amounts to 150—200, whereas in ANGELIN's diagram (1878 a, Pl. 12, fig. 20) of *Heliocrinites prominens* there are not more than about 40. It deserves mentioning that ANGELIN's species was not listed as a synonym of *Heliocrinites araneus* by HECKER (1923, p. 53).

A specimen designated as *Caryocystites* sp. by WIMAN (1907 a, p. 120) was said to approach to *Heliocrinites prominens* but differ in having smaller plates and in being devoid of "die erhöhten Kanten und Ecken der Porenrauten". The present writer has not examined this specimen. The pavement of the theca seems to be more irregular, however, than in our specimens, as far as discernible in the latter ones.

**Remarks** on two specimens referred tentatively to *Heliocrinites prominens*: — Both specimens are in a bad state of preservation. One of them [in SGU] is deformed, especially in the upper portion of the theca. The plates, with prominent umbos and smooth radiating ridges, recall very much the plate-structure of *Heliocrinites prominens* as represented in ANGELIN's Pl. 12, fig. 21 and Pl. 28, fig. 11. — In the second specimen [RM Ec 2386] the test is largely destroyed, but in some plates a structure similar to that just mentioned can be traced. The following measurements were obtained: — height of the theca 30.5 mm; greatest diameter 25 mm; diameter perpendicularly to the preceding, 23 mm. The mouth is an elongated slit with one brachiole-facet at each end. The anus (diam. about 4 mm) lies in a vertical plane about 45 degrees to the left of the vertical plane sectioning mouth and gonopore. It is placed in a small elevation of the theca just where the wall takes a vertical course. In the base of the theca there is a cicatrix of a very faint stem.

In spite of the bad state of preservation of the specimens and the insufficient knowledge of *Heliocrinites prominens*, the writer considers it to be justified to refer them tentatively to this species.

**Regional distribution**: — Sweden, Dalarna: Furudal (the SGU-specimen; the label on the other one gives no locality). — ? The North Baltic area, boulders (WIMAN 1907 a).

**Stratigraphic range**: — Chasmops limestone, Lower Llan-deilian.

### *Heliocrinites stellatus* n. sp.

Pl. 6, fig. 11.

**Derivation of name**: — From Lat. *stellatus*, set with stars, alluding to the very prominent stellate ornament of the thecal plates.

**Holotype**: — UM ec 146.



**Type locality:** — Boda (?), Dalarna.

**Type stratum:** — Boda limestone (?), Upper Ordovician or Lower Silurian.

**Material:** — One unique specimen, the holotype.

**Diagnosis:** — A species of *Heliocrinites*, the theca of which is ovoid, irrespective of the neck-like peristomal projections; thecal plates arranged in about 9 irregular circlets; total number of thecal plates about 90; ambulacral area triangular, with 3 brachiole-facets; anus large, to the left of (and below) the gonopore, which opens in a quadrangular protuberance at the base of the peristomal projection; stem faint.

**Description:** — General shape of the theca. The theca — irrespective of the neck-like peristomal projection — is ovoid, but somewhat asymmetric, so that the left lateral wall is more ventricose than the right one.

**Measurements.** Height of the theca 31 mm; greatest diameter 22 mm; diameter perpendicularly to that mentioned, 20 mm.

**Thecal skeleton.** The base of the theca is pentamerous, which is also true of the peristome. The circlet below the peristome consists of 6 plates. The rest of the thecal plates are disposed in about 8 irregular circlets. In all, the theca is made up of 91 plates. Their approximate distribution among the several circlets, beginning with the basal circlet, may be given thus: — 5, 10, 11, 15, 18, 13, 8, 6, 5. Most plates are heptagonal or hexagonal.

**Surface structures of stereom.** The plates are extraordinarily stout, being provided with thick umbos and strong ornament of broad axial ridges. Between these are deeply depressed triangular fields. The gonopore is surrounded by a strong armour.

The pores of the thecal plates are as a rule not well visible. The tangential pore-canals are developed in the axial ridges, usually 1—3 only in each ridge, as it seems.

The ambulacral area is triangular and has a brachiole-facet at each angle.

**Alimentary canal.** The mouth is lunate with a length of 5 mm. The anus is sub-circular (diameter 4.5 mm), reaching with its lower margin just below the limit of the upper third of the theca. It is situated in a vertical plane to the left of that in which the gonopore is located but not very remote from it.

The gonopore is subcircular, too, its diameter being about 1.5 mm. It opens in a quadrangular stereomatic protuberance below the peristomal projection.

The base-surface of the theca is rounded but the very basal circlet forms

a small projection. The diameter of the stem might have exceeded 1 mm but very slightly.

**Discussion:** — *Heliocrinites stellatus* cannot be mistaken for any congeneric species known to the writer. In surface structures of the stereom it has some resemblance to *Heliocrinites balticus* EICHWALD but is easily distinguished i.a. by the projecting peristome. Certain forms of *Heliocrinites ovalis* (ANGELIN) display a superficial similarity to *H. stellatus* in the general shape of the theca (Pl. 6, fig. 9). The species mentioned is otherwise distinguished by a lot of characters such as number of thecal plates, structure of the pore-system, &c.

**Regional distribution:** — Sweden, Dalarna: Boda(?).

**Stratigraphic range:** — Boda limestone (?), Upper Ordovician and (or) Lower Silurian.

### *Heliocrinites variabilis* n. sp.

Pl. 6, figs. 1—6.

**Derivation of name:** — The specific name *variabilis* was chosen on account of the great variation in shape and, less pronouncedly though, in ornament.

**Holotype:** — RM Ec 1854.

**Type locality:** — Kallholn, Dalarna.

**Type stratum:** — White, splintery Boda limestone, Upper Ordovician or Lower Silurian.

**Material:** — No perfect specimen is present. Some 50 more or less fragmentary and damaged specimens [most of them in RM and SGU] seem to be referable to this polymorphous species.

**Diagnosis:** — A species of *Heliocrinites* with elongate theca, the height of which approaches or even slightly exceeds twice the greatest diameter; thecal plates arranged in 7—10 tolerably regular circlets; plates large in the equatorial zone, smaller towards the poles, covered with an epithek; their number may amount to about 80; anus on a distinct projection, as well as the gonopore, these two openings being located approximately in one and the same vertical plane.

**Description of the holotype:** — The general shape of the theca might be described as elongated pyriform. Thus the lower portion of the theca is swollen, with rounded base, whereas the theca tapers in oral direction so that its diameter becomes less than one fifth of the greatest diameter in the equatorial plane. The theca is somewhat compressed in antero-posterior direction, on account of which it looks narrower in lateral view. The very top of the theca is not preserved, because of which the figure

representing the height of the theca given here would have been somewhat greater, had the specimen been perfect. The holotype is the largest of the specimens not too fragmentary.

**Measurements.** Height 52 mm; greatest diameter 27.5.

**Thecal skeleton.** The arrangement of the plates cannot be made out quite definitely, for the greatest part of the test is lacking on the anterior side. Anyhow they are set in about 9—10 tolerably regular circlets of 6—9 (or perhaps even more) plates in each. The lowest number of plates in the circlets is of course to be found towards the poles, where the plates are minor also, their width being 3—4 mm only; the large plates of the middle thecal region attain a width of 12 mm. Most plates are hexagonal but variations are frequent in this respect. The total number of plates might be estimated at about 80.

**Surface structures.** The plates are covered with an epithek similar to that of *Echinospaerites*. As a matter of course the pore-canals are but slightly visible. The epithek has a well-marked ornament of concentric lines. Axial ridges radiate from the pointed umbo of certain plates, although this feature is less prominent in the holotype than in several other specimens referred to this same species.

**Pores of the thecal plates.** The tangential canals connecting the pores seem to be fine and rather crowded, as far as they could be made visible by etching with diluted hydrochloric acid. They are short, however, so that they do not reach the central area of the plates.

**The ambulacral area and the mouth** cannot be studied, for the top of the theca is wanting, as mentioned above.

**The anus** is a pentagonal aperture measuring 5 mm in diameter. The anal pyramid is not preserved. The anus, which is surrounded by 6 plates, opens on a roughly quadrangular elevation, tolerably at the limit for the upper third of the theca.

**The gonopore** is damaged but may be traced 7—8 mm above the anus, probably separated from it by two plates. They lie in the same vertical plane.

The test is absent on the very base surface, too. So nothing can be stated about the stem. The base-surface is rounded.

**Remarks on typoids:** — There are a number of specimens, which agree essentially with the holotype of *Heliocrinites variabilis* but deviate in different respects. Thus, in some forms, the theca is more elongated, its lower portion not being ovoid but tapering in basal direction too (Pl. 6, fig. 3). RM Ec 2172 (Pl. 6, fig. 2) is intermediate in this respect. In cases of minor relative width it may happen that the height of the theca exceeds twice the greatest diameter, by which the theca approaches in general shape that of *Caryocrinites*. This is true e.g. of the species just referred to [RM Ec

1865], but the anus is situated well within the upper third of the theca, which, according to the diagnoses of *Heliocrinites* and *Caryocystites* here adopted, excludes our form from the latter genus.

It is possible to procure measurements of a few specimens only, owing to the generally fragmentary state of the thecae available. Only in two juvenile specimens [UM ec 90 a; spec. in SGU] the theca is almost complete. In the following table measurements are given for these and two more specimens.

| (Measurements in mm)      | Specimen<br>in SGU | UM ec<br>90 a | RM Ec<br>2671 | RM Ec<br>2172 | RM Ec<br>1865 |
|---------------------------|--------------------|---------------|---------------|---------------|---------------|
| Height of the theca ..... | 14                 | 18            | > 35          | 42            | about 48      |
| Greatest diameter .....   | 8.2                | 9             | 20            | 22            | » 22          |

The number of plates cannot be estimated for the two immature specimens. In RM Ec 2671 and 1865, which may be regarded as medium-sized, the number of plates might have been about 60. The largely exfoliated specimen RM Ec 2172 shows the sutures very clearly; it has about 70 plates. The pavement of the posterior side is in general composed of larger plates than that of the anterior one.

In several specimens the sculpture of the plates is decidedly more pronounced than in the holotype. In the forms alluded to, the axial elements are more strongly developed, and the eminences for anus and gonopore are more protruding (cf. Pl. 6, figs. 4—5).

The tangential pore-canals are well exposed in an exfoliated specimen [in SGU], Pl. 6, fig. 6. In this small specimen they are not so crowded as seems to be the case in the holotype.

The actinal region is preserved in the SGU-specimen referred to in the table of measurements. It shows a small triangular area, in the angles of which is a brachiole-facet. There are no covering plates. The abactinal region seems to consist of a circlet composed of 6 or 7 elongated plates. The point of attachment for a circular stem with small diameter is also visible.

The location of the anus is not quite constant in all specimens. Generally the anus lies within the upper third of the theca or close to it. But in UM ec 90 a, e.g., it is just above the middle of the theca. This, however, might be an anomaly rather than a feature characteristic of immature stages, for in the still smaller SGU-specimen the anus holds a higher position, although somewhat below the upper third of the theca. Further there are adult specimens (e.g. RM Ec 2172), in which the anus lies immediately below the upper third of the theca. — In the specimen figured in Pl. 6, fig. 2, the anus shows a short proboscis-like structure, but the writer is not sure that it really belongs to the theca.



**Discussion:** — The broader forms of our species as represented by e.g. the holotype reveal a rather considerable similarity to *Heliocrinites rouvillei* (KOENEN) (1886, Pl. 8, fig. 4) from beds of Caradocian age at Montpellier, France. This species differs i.a. in the following respects: — the theca is hardly pyriform but rather ovoid; the number of thecal plates is greater (about 110); the mouth opens in a conic peristome; the rounded anus is not situated on an elevation.

BATHER (1906, p. 18) pointed out that *Heliocrinites rouvillei* as described and figured by JAEKEL (1899, p. 330, Pl. 10, fig. 5) can hardly be identical with KOENEN's species but should certainly be regarded as distinct from *H. rouvillei* (KOENEN). BATHER seems to have adduced sufficient reasons for his proposal. But it should be noted that, in the same way as the broad forms of our species are reminiscent of *Heliocrinites rouvillei* (KOENEN), the elongate forms, for their part, have some similarity to *Heliocrinites rouvillei* (JAEKEL, non KOENEN). In specimens with stronger sculpture this similarity is further increased. Yet the ornament seems in our species not to be as prominent as in JAEKEL's form, in which the thecal plates are likewise covered with an epithek. The elevation for the mouth is differently shaped in JAEKEL's species. There is no aperture between the mouth and the anus.

KOENEN (1886, p. 248) deliberated upon placing his species in a separate genus. Yet this, and our Swedish species, may be retained in *Heliocrinites*. As for the latter it was indicated above that, in some respects, it comes closer to *Caryocystites* than to typical representatives of *Heliocrinites*.

Finally it may be mentioned that a few specimens referred to *Heliocrinites variabilis* display some similarity to the dubious "*Megacystis*" *ovalis* ANGELIN (1878 a, Pl. 27, fig. 13). This may be said about RM Ec 1851 and the SGU-specimen figured in our Pl. 6, fig. 6.

It is possible that SCHMALENSÉE (1892, p. 499) alluded to specimens of *Heliocrinites variabilis* in referring to "*Caryocystis* cfr *testudinaria* HIS." in a list of fossils from Lissberg.

### *Heliocrinites* n. sp.

Pl. 6, fig. 13.

1918 *Caryocrinites* sp. — TROEDSSON, p. 21.

**Holotype:** — The specimen figured in Pl. 6, fig. 13 [LM].

**Type locality:** — Tommarp, Scania.

**Type stratum:** — Grey clay-shale belonging to the zone of *Staurocephalus clavifrons*, uppermost Ordovician.

**Material:** — One unique specimen, the holotype.

**Remarks:** — The present form has not been denoted by any spe-

cific name, though undoubtedly representing a new species. The reason for this measure is that the theca, in several respects, is too badly preserved as to admit the bringing forward of a clear diagnosis.

The theca is strongly compressed and crushed partially. It seems to have been ovoid, with a height of about 24 mm. The number of plates can be estimated at about 60. Main axial ridges run to the angles of the plates; between these there is an ornament of fainter ridges. The ambulacral area and the mouth seem to have been triangular, the first-mentioned bearing probably 3 brachiole-facets. Anus and gonopore could not be detected, nor the point of attachment for an eventual stem.

TROEDSSON (1918, p. 21) proposed this species to be a representative of *Caryocrinites*. After removing the matrix around the actinal region of the theca, it became evident at once, however, that it cannot possibly belong there. Instead, the shape of the ambulacral area, the ornament on the plates, and the general shape of the theca, induce us to refer the species to *Helio-crinites*.

The form is interesting as one of the very few cystoids known from Scania.

#### Family *Echinosphaeritidae* NEUMAYR 1889, emend. JAEKEL 1918.

The systematic disposition of the forms of this family is not quite clear in all respects. BASSLER (1938, p. 9) — following BATHER (1906, p. 13) — ranked *Arachnocystites* NEUMAYR as a separate genus, whereas it was taken as a synonym of *Echinosphaerites* by JAEKEL (1899, p. 332), HECKER (1923, p. 13), and ZITTEL-BROILI (1924, p. 214). *Deutocystites* BARRANDE was placed by BASSLER (1938, p. 8) with the *Aristocystitidae* (see also p. 30 above). This genus, too, was regarded by JAEKEL, HECKER, and ZITTEL-BROILI as identical with *Echinosphaerites*. As far as can be inferred from figures of these Bohemian Middle Ordovician forms delivered by BARRANDE (1887), JAEKEL's point of view seems to be well justified. But the present writer thinks it wise not to give a definite opinion of the matter, having had no occasion to study the forms in question. The identification with *Echinosphaerites*, therefore, may be looked upon as provisional.

*Palaeocystites* BILLINGS, as pointed out by BATHER (1906, p. 14), is a dubious member of the family, being still very imperfectly known. It was described from the Chazyan (lower part of the Middle Ordovician) of N. America. Whether *Palaeocystites bessarabianum* VÂSCĂUȚANU (1931, pp. 564, 654), from the Upper Ordovician and adjacent part of the Middle Ordovician in Roumania, is congeneric with the American form, the writer cannot decide.

Genus *Echinosphaerites* WAHLENBERG 1818.

Genotype: — *Echinus aurantium* GYLLENHAAL 1772.

Synonyms: — See ANGELIN 1878 a (p. 28), JAEKEL 1899 (p. 331), BASSLER 1938 (p. 91).

Regional distribution: — Sweden, Norway,<sup>33</sup> Estonia, USSR, Poland,<sup>34</sup> N. Germany (drift boulders),<sup>35</sup> Thuringia,<sup>36</sup> Great Britain,<sup>37</sup> N. America,<sup>38</sup> Yunnan,<sup>39</sup> Belgium,<sup>40</sup> Bohemia.<sup>41</sup>

Stratigraphic range: — Middle—Upper Ordovician. All species made known except those from Belgium and Bohemia are Middle Ordovician.

Representatives of *Echinosphaerites* were among the first cystoids to be known and described (cf. p. 1 seq. above). The first attempt at a general survey of the contents of the genus was made by JAEKEL (1899, pp. 336—337). His classification was mainly based on differences in the shape of the theca. The Russian material of *Echinosphaerites* was elaborated by HECKER (1923). With regard to the development of the pore-rhombs, two "mutations", *infra* and *supra*, were recognized within *Echinosphaerites aurantium* (GYLLENHAAL). These "mutations" were shown to be confined to distinct stratigraphic horizons. ORVIKU (1927 a), dealing with material from Estonia, confirmed the results reached by HECKER.

A rather extensive material of *Echinosphaerites* from Sweden was available to the writer. There is a striking difference in the state of preservation of specimens from different areas. Thus the material from Västergötland presents itself — almost without exception — in the state of moulds, whereas in specimens from other areas in Sweden the test is generally more or less preserved. In specimens from the Chasmops limestone of Öland all or some of the "primary pores" are obliterated (secondarily) almost regularly, which must be due to the intimate connexion between the fossils and the surrounding rock. Clean specimens of *Echinosphaerites aurantium* weathered out are sparse at Böda Harbour which is the principal locality for Lower Chasmops limestone in Öland.

<sup>33</sup> SCHLOTHEIM 1826 (column 312); KJERULF 1865 (p. 4); BRÖGGER 1882 (p. 42, footnote 1), 1887 (pp. 17, 23); KLÆR 1927 (pp. 2, 15), 1932 (pp. 22, 28—29), STØRMER 1930 (p. 76), 1934 (p. 331).

<sup>34</sup> CZARNOCKI 1928 (p. 577).

<sup>35</sup> KLÖDEN 1834 (p. 241); JAEKEL 1899 (p. 336).

<sup>36</sup> LORETZ 1884 (p. 141); FREYBERG 1923 (pp. 248, 263).

<sup>37</sup> FORBES 1848 (p. 516); TÖRNQUIST 1879 (p. 71); MARR 1882 (p. 325); JAEKEL 1899 (p. 337).

<sup>38</sup> BASSLER 1911 (pp. 14, 27), 1919 (p. 139); FOERSTE 1920 (p. 38).

<sup>39</sup> REED 1917 (p. 13).

<sup>40</sup> JAEKEL 1899 (p. 337); BATHER 1913 (p. 494, § 559).

<sup>41</sup> JAEKEL 1899 (p. 337).

Already from a superficial survey it is obvious that the material is not undifferentiated; rather it is fairly polymorphous. Although, on the whole, the bulk of the specimens available gives a unitary impression, variations in size and shape of the theca, in the development of the plates and the pore-rhomb, in location of the gonopore, &c. are easily proved.

The stratigraphic appearance of the so-called mutations of *Echinospaerites aurantium* in Estonia is well known from investigations carried out by ORVIKU, as just mentioned. ORVIKU (1927 a, p. 15) suggested that a fresh study of the Scandinavian Echinospaeritidae, "besonders des stratigraphischen Materials", would reveal an evolutionary series which could be put in connexion with the East Baltic form-series. Unfortunately the very conditions for gaining such a result from an investigation of the Swedish museum-material are not to hand. On account of lacking or inadequate labelling it is namely, in general, impossible to make out whether certain trends have guided the development in the course of time, or whether a free variation has taken place. After removing *Echinospaerites aurantium suecicus* JAEKEL, which is well defined stratigraphically, and certain specimens characterized by their very large size, the writer cannot see any other possibility than simply to refer the rest of the Swedish material to the nominate form of *Echinospaerites aurantium*, yet calling attention to variations in different respects.

*Echinospaerites aurantium aurantium* (GYLLENHAAL 1772).

Pl. 1, fig. 4. Pl. 7, figs. 2—7. Pl. 8, figs. 1, 3—4. Text-figs. 1: 4—5; 2: 6—9; 3: 17.

- 1772 *Echinus Aurantium*. — GYLLENHAAL, p. 253, Pl. 8, figs. 4—5; Pl. 9, figs. 6—9 [figs. 5—6 inverted].  
 1818 *Echinospaerites Aurantium*. — WAHLENBERG, p. 44.  
 1821 *Echinospaerites Aurantium*. — WAHLENBERG, p. 52.  
 1828 *Sphaeronites pomum* (ex parte). — HISINGER, p. 196, Pl. 5, figs. 2—3.<sup>42</sup>  
 1837 *Sphaeronites Citrus*. — HISINGER 1837 b, p. 91, Pl. 25, figs.  
 1878 *Echinospaera aurantium* GYLLENHAAL. — ANGELIN 1878 a, p. 28, Pl. 14, figs. 1—13, ? 14—18, 19—21; Pl. 28, figs. 9, 9 a.  
 1888 *Echinospaera aurantium* GH. — LINDSTRÖM 1888 a, p. 16.

In this list, papers only referring reasonably to *Echinospaerites aurantium aurantium* are contained. Mere mentions in regional descriptions &c. were omitted. As to references to this species in writings of certain authors of old times, see pp. 1 and 4 above.

<sup>42</sup> The specimen figured in HISINGER 1828, Pl. 5, fig. 2, is to be found in the HISINGER collection [RM Ec 5742]. It is a strongly worn theca to which a fragment of a crinoid stem is attached, as observed by HECKER (1923, p. 9). This stem was thought by HISINGER to be connected organically with the theca. It was refigured in HISINGER 1837 b, Pl. 25, fig. 8 a. This figure is extremely embellished.



HECKER (1923, p. 14) suggested that the Scandinavian *Echinospaerites aurantium* is possibly not represented in the East Baltic area. Here the nominate-form is replaced by the "mutations" *infra* and *supra*. Lists of synonyms of these forms were presented by HECKER (1923, pp. 16—17, 25).

As mentioned above (p. 4, foot-note 5), GYLLENHAAL's original material is likely to be considered as lost. Yet there is maybe a small chance that some specimen from the GYLLENHAAL collection will happen to be traced. Until such a specimen will be brought forth, it might be suitable to select a provisional neotype. GYLLENHAAL's species was based on specimens from an unknown locality in Västergötland. The neotype, therefore, has to be chosen among specimens from this province, although these are constantly in no favourable state of preservation. The author proposes to designate as neotype the specimen RM Ec 3030, which agrees tolerably with GYLLENHAAL's figs. 4—7. — No specimens figured by ANGELIN (1878 a) could be identified so far.

Type locality: — Not known (Västergötland).

Type stratum: — Chasmops limestone, Middle Ordovician.

Material: — Some 800 specimens were available to the writer.

Diagnosis: — A subspecies of *E. aurantium* with spheroidal theca (exclusive of polar projections) of moderate size (most specimens varying between 25 and 45 mm; theca composed of a great number (many hundreds) of polygonal plates strongly varying in shape and size; oral pole more or less projecting; pores connected by compound canals (usually 2—4 tangential canals connecting one pore at each side of the suture); pore-rhombs as a rule reaching, or approaching, the plate-centres,<sup>43</sup> which means that the y-axis (parallel to the suture crossed by the tangential pore-canals) of the pore-rhomb is shorter than the x-axis; the lines connecting the mouth and the gonopore (o—g), the gonopore and the anus (g—a), and the anus and the mouth (a—o) are in the average-ratio 1 : 1.6 : 2.3; stem very feeble, its diameter being  $\frac{1}{12}$  or less of the diameter of the theca.

Description: — General shape of the theca. The theca is spheroidal, irrespective of the peristomal and an eventual basal projection. Now the height exceeds the diameter by one or a couple of millimetres, now it is the contrary. The peristome regularly rises over the general surface of the theca, forming a more or less chimney-like projection ("collum", ANGELIN 1878 a). Not seldom the aboral pole is somewhat produced, too. Exceptionally, this has the character of a gradual tapering of the theca (cf. Pl. 7, fig. 4). By this, the theca assumes some resemblance to *Echinospaerites pirum* JAEKEL 1899, which is yet curved otherwise than the specimen just referred to and, further, seems to have short tangential pore-canals.

<sup>43</sup> This character varies even in one and the same specimen.

HECKER (1923, p. 36), moreover, rightly called in question whether the so-called *Echinosphaerites pirum* is specifically distinct.

Most specimens belong in the size-class 25—45 mm.

The thecal skeleton consists of a very great number of plates. By counting the plates in one half (the other half is damaged) of the specimen figured in Pl. 7, fig. 6, the total number was estimated at 800—850. According to the size of the theca and the size of the separate plates the total number of plates varies considerably in different specimens, however. A plan for the arrangement of the plates cannot be made out. JAEKEL (1899, p. 336) proposed the basal circlet in *Echinosphaerites aurantium* (probably not the nominate-form) to contain 4 plates, which, according to ORVIKU (1927 b, p. 11) is true of the "mutation" *supra*, whereas there is a greater number in the "mutation" *infra*. In the Swedish specimens it is possible to analyse the basal circlet but occasionally. Thus in eight instances only the present writer met with such specimens, six of them having 6 plates and two of them having 7 plates. — A detail-figure of the "collum", i.e. the peristomal projection, was communicated by ANGELIN (1878 a, Pl. 14, fig. 4). The present author cannot judge whether the construction of this portion is represented correctly in the figure mentioned, the specimen from which it was drawn not having been traced. In by far the greatest number of specimens examined by the writer there is no chance to get an idea of the arrangement of the plates in this portion of the theca. But in cases where the sutures are discernible with some degree of certainty, the terminal plates supporting the ambulacral area seem to be elongated pieces (5 or 6 in number?).

A glance at Pl. 7, fig. 6, will prove that the thecal plates are very polymorphous. There are all sorts of plates, from triangular to polygonal ones with 10 sides. The variation in size is considerable. The increase of the theca obviously took place in the first hand by the insertion of new plates, whereas the growth of older plates was rather limited, as observed by HECKER (1923, p. 17) concerning the "mutation" *infra*.

GYLLENHAAL (1772, p. 249) already distinguished two varieties of *Echinosphaerites aurantium*, one called  $\alpha$ , in which the separate plates are very unequal in size, and one variety  $\beta$  with approximately equal-sized plates (cf. text-figs. 1—2, pp. 2—3 above). In the last-mentioned case the theca might have attained a certain degree of stability as to the increase of the skeleton. Specimens constituting the  $\alpha$ -form, on the other hand, must have been in a state of expansion with abundant growth of new plates.

The epithek concealing the pore-rhombs is often preserved altogether or in part. It is generally smooth. Concerning the state of preservation of material from different areas, see p. 139 above.

Pores of the thecal plates. The pores, which are immersed in the stereom, are especially well visible on moulds, where they often appear

as granules or short pegs, being casts of the vertical pore-canal. These are usually arranged around the centre of the plate, but, as mentioned, a certain variation in this respect is noticeable even in one and the same specimen. In consequence of the location of the pores more or less at the plate-centres, the pore-rhombs extend over the main part of the plates. Thus the y-axis of the pore-rhombs is generally shorter than the x-axis. ORVIKU (1927 b) was able to show — in the case of the “mutation” *infra* as well as the “mutation” *supra* — how in Estonia variations in the shape of the pore-rhombs are correlated with the stratigraphic and regional appearance. The differences in development of the pore-rhombs were put in connexion with facial conditions making different demands on the capacity of the respiration-system. A similar classification of the Swedish material into groups fixed stratigraphically could not be realized for reasons emphasized above. Nor is there any marked difference in specimens from the several distribution-areas, should it not be a certain increase in the frequency of shorter pore-rhombs in specimens from Öland. — The tangential canals connecting the pores are as a rule compound, 2—4 of them extending between each two pores.

The ambulacral area is elevated over the theca by means of the peristomal projection. Its details are usually not traceable. In the few instances where this was possible, the ambulacral system proved to be tetroradial (Pl. 8, fig. 3) or triradial. The presence of ambulacral areas with 6—8 brachiole-facets like those figured by ANGELIN (1878 a, Pl. 14, figs. 8—9; Pl. 28, fig. 9 a) was not confirmed. The structure of the pavement of the ambulacral area is not visible in any specimen available.

Alimentary canal. In consequence of the bad state of preservation of the ambulacral area, the mouth is not directly visible. Most likely it has had the shape of an elongated slit. The anus is pentagonal in all specimens examined by the writer. An anal pyramid of 5 valvules is very often preserved. The anus is situated in a vertical plane to the left of that in which the gonopore lies, and within the upper third of the theca. Anal pyramids with a divergent number of valvules have been met with in material from foreign areas (JAEKEL 1899, p. 334; see also our Pl. 8, fig. 2, showing an anal pyramid with 4 valvules).

The gonopore is rounded or triangular, its diameter being about the half of that of the anus. In one instance only [RM Ec 2417] the covering plates were observed, forming a flat pyramid of 3 valvules.

The mutual relations in position between mouth, gonopore, and anus were determined by measuring the lines connecting these apertures. It turned out that the lines mentioned (o—g : g—a : a—o) are in the average ratio 1 : 1.6 : 2.3, which was counted on the basis of measurements of 45 specimens, 15 from each of the provinces Västergötland, Östergötland, and Dalarna. When taken separately, the figures for the specimens from Öster-



götland are somewhat below the average, viz. 1 : 1.5 : 2.2. But rather considerable variations in the length of the lines in question could be stated for material from all areas. Further it should be observed that exact measurements (in the first hand of o—g and a—o) could not be secured on account of the generally imperfect state of the oral projection.

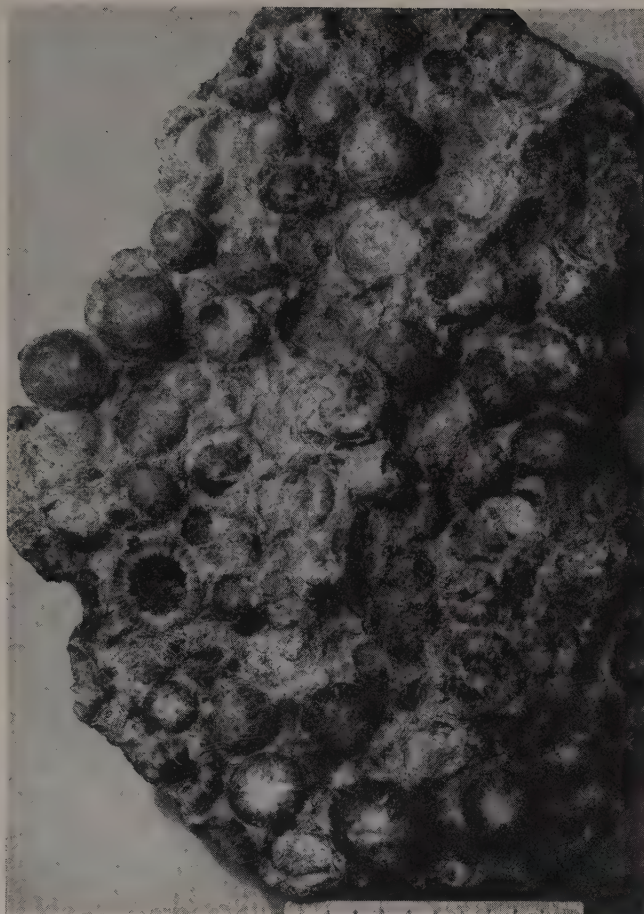
A very feeble, thread-like stem has been present; maybe it was quite lacking under certain circumstances.

Concerning structures proposed by JAEKEL to be mesenteric septa, see pp. 55—56 above.

**D i s c u s s i o n:** — It was pointed out repeatedly above that the Swedish material of *Echinosphaerites aurantium* in main does not admit of a dividing into stratigraphically fixed varieties or "mutations". Undoubtedly our forms are most nearly related to East Baltic forms with well-developed pore-rhombs. It is remarkable that in certain respects — number of plates in the basal circlet, interrelations of the "primary pores" — the Swedish material agrees more with the "mutation" *infra* than with the "mutation" *supra* (in the last-mentioned there are 4 plates only in the basal circlet, and the ratio o—g : g—a : a—o is 1 : 2.3 : 2.6; ORVIKU 1927 b, p. 11). The "mutation" *infra* in Estonia is distributed in the Aseri- ("Echinosphaerites"-) zone (ORVIKU 1927 a, p. 15; 1927 b, pp. 3—4; 1940, p. 44), but does not pass into the superimposed Lasnamäe- ("Baukalkstein"-) zone. The Swedish equivalents to these divisions are the zones of *Asaphus platyurus* and *Illaenus schroeteri* ("chiron"), which means that the "mutation" *infra* is confined to a horizon decidedly below the *Echinosphaerites*-bearing Lower Chasmops limestone of Sweden. — The "mutation" *supra* in Estonia occurs in the topmost Uhaku ("Caryocystites"-) zone and, mainly, in the Kukruse. This stage and the Itfer correspond to the Lower Chasmops limestone. The *Echinosphaerites*-forms of the Itfer have not been studied closely as yet.

*Echinosphaerites aurantium* has a wide distribution. BASSLER 1911, p. 27) reported "specimens of *Echinosphaerites* which can not be distinguished from the common Baltic species" occurring in the Kimmswick formation in eastern Missouri (Trenton, and topmost Black River ?, Lower Caradocian). In 1919 (p. 207) BASSLER described *Echinosphaerites aurantium americanus* from other areas of N. America. BASSLER remarked that this form is more ovate than the European *Echinosphaerites aurantium*, which is also true of a few specimens from Virginia [RM] examined by the writer. — *Echinosphaerites sinensis* REED, from the Middle Ordovician of Yunnan, was said by REED (1917, p. 15) to have a close resemblance to *Echinosphaerites aurantium* in spite of several distinguishing features being mentioned. A poorly preserved cystoid was designated as *Echinosphaerites* cf. *aurantium*, having the "pore-canals arranged precisely in the manner indicated by JAEKEL in one of his figures". The figure referred to is Pl. 8,





Text-fig. 17. *Echinospaerites aurantium aurantium* (GYLLENHAAL). A piece of rock with crowded specimens [LM].  $\frac{1}{2.8}$  (approx.). — Öland: Boda Harbour.

fig. 11, in JAEKEL 1899, which according to HECKER (1923, p. 29) represents *Echinospaerites aurantium* "mutation" *supra*.

*Echinospaerites*, as is well known, is often found in limestone-beds crammed with thecae (text-fig. 17).<sup>44</sup> The origin of these associations will not be discussed at length here; it may only be mentioned that different opinions of their formation are thinkable. Either they are autochthonous or allochthonous. In the first case we have to assume that these cystoids lived in immense colonies at the places where they are found now. This

<sup>44</sup> HOLM (1901, pp. 55—56) called attention to the noticeable fact that no true cystoid-limestone is developed in the Chasmops series of the Kinnekulle Mountain in Västergötland. Here *Echinospaerites* is namely relatively sparse and in no way rock-forming. The statement was confirmed by WESTERGÅRD (1943, p. 77). — In the old quarries, no more accessible, at N. Freberga in Östergötland, real cystoid-beds were exposed (TÖRNQUIST 1875, p. 66; JÖNSSON 1887, p. 19).

opinion was advanced e.g. by DEECKE (1915, p. 3; 1916, p. 6) and HADDING (1933, p. 52). The last-mentioned author indicated certain environmental conditions controlling the flourish and sudden disappearance of the cystoids. In the second case the *Echinosphaerites*-beds have to be looked upon as thanatocoenoses. BATHER (1928 b, p. LXXVIII) wanted to make out that the thecae of *Echinosphaerites* were anchored like captive balloons by means of a flexible and tensile stem. "When dead, and occasionally in life, the thecas would have broken away from their moorings and have been swept by currents into heaps along the shore." BATHER (1928 b, p. LXXX) further pointed out that the world-wide distribution of *Echinosphaerites* with little if any specific change could be declared by assuming a planktonic mode of life of these organisms. Yet on a preceding page BATHER himself had emphasized certain objections to the hypothesis. The thought of *Echinosphaerites* as a planctonic (or maybe partly nectonic) organism was first promoted by KIRK (1911, pp. 7—8). As the evidence of sedimentary petrology speaks in favour of an autochthonous origin of the cystoid-beds, this point of view seems to be best supported. The distribution over great areas, then, must have been effected by means of larvae transported by currents. KIRK's objection (1911, p. 8) that a similar dispersal power would equally have been characteristic of the larvae of related forms is hardly decisive.

**Regional distribution:** — Sweden, Västergötland: Ekberget (Kinnekulle), Jonstorp (Mösseberg),<sup>45</sup> Ljungstorp, Rustsäter (Kinnekulle), Verlaskog (the localities mentioned verified by museum specimens), Nyckelängen (Älleberg; WALLERIUS 1894, p. 299), NW of Ryd (WESTERGÅRD 1928, p. 47). — Östergötland: Borghamn (boulders), Motala, N. Freberga, Skarpåsen (boulders). — Öland: Böda Harbour, Dödevi. — Dalarna: Amtjärn, Boda, Enån, Fjäckä, Furudal, Gulleråsen, Kallholn, Kårgårde, Lenåsen, Orsbleck, Osmundsberg, Skattungbyn, Slättberg, Sollerön, Stenberg (boulders), Vattnäs, Vika, Vikarbyn, Åberga, Östbjörka (all localities mentioned verified by museum specimens), the canal between Amtjärn and Glisstjärn (E. WARBURG 1910, p. 449), Nittsjö (TÖRNQUIST 1874, p. 14). — Jämtland: Högbro at Hårkan, Johannisro (Mörsil, boulders), E of Locknesjön (boulders), Norderön (boulders) (the localities mentioned verified by museum specimens), Lit (THORSLUND 1940, p. 105, foot-note 1), Slandrom rivulet (ibid., p. 22), Torvalla (ibid., p. 19), Vallmyra (ibid., p. 20), Åsarna (ibid., p. 68), Åskott (ibid., p. 93). — N. Baltic area: boulders collected at Harg, Simpnäs, Sunnersta, Ö. Edsvik (all in Uppland; WIMAN 1907 a, p. 120).

Distribution of forms nearly related to the nominate form: Norway. — Estonia. — USSR. — Poland. — N. Germany (drift boulders). — Great Britain. — N. America. — Yunnan.

<sup>45</sup> Specimens from Chasmops limestone labelled Kleva ("Klëfva") are likely to have been collected at the same locality as those labelled Jonstorp; cf. LINNARSSON 1869, p. 45.

**Stratigraphic range:** — Lower Chasmops limestone, Upper Llandeilian.

TÖRNQUIST (1874, p. 14; 1875, p. 66) asserted that, upon the whole, *Echinosphaerites aurantium* holds a somewhat lower stratigraphic position than *Heliocrinites granatum*, although it occurs along with that species also. Yet in 1889 (p. 314) he stated both species to occur in the middle part of the Chasmops limestone.

According to certain statements, *Echinosphaerites aurantium* would also occur in strata below the Chasmops limestone. MOBERG (1890, pp. 16—17) reported a bed crammed with thecae of the species in the hanging wall of the Ancistroceras ("Strombolituit") limestone E of Slagersta (Stenåsa) in Öland. The limestone was interpreted as a passage bed to the Chasmops limestone. The same cystoid-limestone is met with at some other localities also in Öland (WIMAN 1902, p. 30). The present writer has not examined any specimens from this horizon.

Further, LINNARSSON (1871 b, p. 343) mentioned a species from the so-called "leverstenen" (Schroeteri + Ancistroceras limestone, top of the Asaphus series, Middle Llandeilian) which he thought possibly referable to *Echinosphaerites aurantium*. Probably the same species was alluded to as "*Echinosphaerites* sp." by HOLM (1901, p. 52) and WESTERGÅRD (1943, p. 73).

*Echinosphaerites aurantium suecicus* JAEKEL 1899.

Pl. 8, fig. 5.

1890 *Echinosphaera*. — MOBERG, p. 15.

1899 *Echinosphaerites aurantium* var. *suecica* m. — JAEKEL, p. 336.

1906 *Echinosphaera*. — WIMAN, p. 108.

1927 *Echinosphaerites aurantium* var. *suecica*. — ORVIKU 1927 b, p. 13.

It is uncertain whether a **holotype** was designated by JAEKEL. If this was done, its present depository is unknown to the writer.

**Type locality:** — Unknown (Sweden).

**Type stratum:** — Not known with certainty (probably red limestone in the upper part of the Asaphus series). Middle Ordovician.

**Material:** — Some 30 specimens [RM, SGU].

**Diagnosis:** — A subspecies of *E. aurantium* with somewhat ovoid theca of moderate size (seldom exceeding 40 mm); oral pole not projecting; thecal plates with low axial ridges; pores connected by compound canals, 2 tangential canals, as far as observed, connecting one pore at each side of the suture; the length of the y-axis of the pore-rhombs often about equal to that of the x-axis, on account of which the pore-rhombs generally do not extend to the central parts of the plates; ambulacral area (constantly?)



triangular with 3 brachiole-facets; the lines o—g, g—a, a—o are in the average ratio 1 : 1.5 : 2.0; stem feeble.

**Description:** — **General shape of the theca.** The theca is as a rule ovoid, though the difference between the height and the greatest diameter is not very considerable, as appears from the measurements below. JAEKEL (1899, p. 336) stated that the theca tapers in aboral direction. Although clearly defined in some specimens, this feature can hardly be said to be characteristic of the subspecies, as far as can be inferred from the material available. The oral pole is not projecting, the ambulacral area being but slightly elevated over the surface of the theca.

| (Measurements in mm)    | Spec. in<br>SGU | RM Ec<br>4870 | RM Ec<br>4236 | Spec. in<br>SGU | RM Ec<br>4240 | RM Ec<br>4371 | RM Ec<br>4239 |
|-------------------------|-----------------|---------------|---------------|-----------------|---------------|---------------|---------------|
| Height of the theca . . | 43              | 42            | 39            | 37              | 35            | 34            | 30            |
| Greatest diameter . . . | 35              | 38            | 33            | 30.5            | 29            | 28.5          | 28.5          |

Most specimens vary in height between 30 and 40 mm.

**Thecal skeleton.** The number of plates in the thecal skeleton certainly amounts to some hundreds but is hard to estimate owing to the thick epithek usually present. In size and shape the thecal plates seem to have about the same character as in the preceding subspecies. Where recognized, the plates in the basal circlet are 5 (1 case) or 6 (1 case).

The surface of the epithek is raised in low ridges extending from a fairly well-marked umbo to the angles of the plates. Besides, the epithek has a concentric ornament parallel to the outline of the plates.

**Pores of the thecal plates** are visible only where the test is abraded. Owing to impregnation with ferric matter this has namely assumed a strong red colour concealing the structure of the pore-system even after etching with diluted hydrochloric acid. As mentioned in the diagnosis, two pores invariably seem to be connected by 2 tangential canals. The number of such canals in a middle-sized pore-rhomb is 12. As a rule the pore-rhombs do not reach the plate-centre, and the y-axis is about as great as the x-axis.

In all instances where preserved, the ambulacral area is triangular with 3 brachiole-facets (Pl. 8, fig. 5).

**Alimentary canal.** The mouth is not visible in any specimen. The anus (diam. about 5 mm) is pentagonal. In some cases a low pyramid with 5 valvules is preserved.

The gonopore (diam. not exceeding 2 mm) is rounded. Its covering plates were not observed.

The "primary pores" lie somewhat more apart than in the preceding



subspecies. Thus the lines  $o-g : g-a : a-o$  are in the average ratio 1:1.5:2.0 (compared with 1 : 1.6 : 2.3 in the nominate form).

A thread-like stem has been present.

**Discussion:** — By the characters mentioned in the diagnosis this subspecies is sufficiently well delimited from the nominate form. Of other forms known it has in the first hand to be compared with *Echinosphaerites aurantium* “mutation” *infra*, which appears in equivalent strata in the East Baltic area (the Aseri zone). Obviously there is a considerable resemblance — being indeed not very far from identity — especially to the form designated as “mut. *infra-c*” by ORVIKU (1927 b, p. 8), in which the porrhombs seem to be developed in a similar way as in our form. Further, in “mutation” *infra* the height of the theca exceeds the diameter by some mm, and the thecal plates are provided with axial ridges originating from a marked umbo (ORVIKU 1927 b, p. 5). ORVIKU (p. 13) assumed that the Swedish form is an advanced member of the evolutionary line displayed in the “mutation” *infra*. But this assumption can hardly be said to elucidate the relations of *Echinosphaerites aurantium suecicus*, if we consider that this form existed synchronously with the East Baltic “mutation” *infra*. The only distinguishing feature — and by no means a decisive one — apparent from ORVIKU’s description is that the “primary pores” are somewhat less apart in the East Baltic form ( $o-g : g-a : a-o = 1 : 1.6 : 2.2$ ).

The papers of MOBERG (1890) and WIMAN (1906) mentioned in the list of synonyms above contain no indications of the habit of the *Echinosphaerites*-form to which they refer, but on account of its geologic horizon we may safely suppose that the form alluded to was *Echinosphaerites aurantium suecicus*.

**Regional distribution:** — Sweden, Öland: Hulterstad, Lerkaka, Löt (boulders), Mellby, Torp, Vedborm (boulders).

**Stratigraphic range:** — The thecae and attached rock-fragments have the colour typical of fossils and limestones belonging to the zone of *Asaphus platyurus* in the upper part of the *Asaphus* series, corresponding to a lower part of the Llandeilian. The form referred to by MOBERG and by WIMAN was said to occur in a distinct horizon forming a cystoid-limestone in the top of the *Platyurus* zone.

### *Echinosphaerites grandis* JAEKEL 1899?

Pl. 7, figs. 8—9.

? 1899 *Echinosphaerites grandis* n. sp. — JAEKEL, p. 336.

? 1923 *Echinosphaerites Pogrebowi* nov. sp. — HECKER, p. 35, Pl. 2, figs. 4—5.

**Holotype:** — Unknown to the writer.

**Type locality:** — Unknown (neighbourhood of Tallinna, Estonia?).

**Type stratum:** — Unknown.

**Material:** — Some 15 specimens [RM].

**Diagnosis:** — A species of *Echinosphaerites* with sphaeroidal theca of very large size, reaching about 70 mm in diameter; surface of the test smooth.

This diagnosis is the principal contents of the description given by JAEKEL, which is, strictly, too insufficient, as pointed out by HECKER (1923, p. 33).

**Description:** — The general shape of the theca is mainly spheroidal. In some specimens the height exceeds the greatest diameter a little, in others the width is a little greater than the height. A peristomal projection has been present but is not preserved in any specimen available.

| (Measurements in mm)   | RM Ec<br>2393 | RM Ec<br>3279 | RM Ec<br>3276 | RM Ec<br>2277 | RM Ec<br>2699 | RM Ec<br>3271 | RM Ec<br>3280 |
|------------------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|
| Height of the theca .. | 74            | about 70      | 68            | 66            | 65            | about 60      | 56            |
| Greatest diameter .... | 65            | 68.5          | 73            | 70            | 67            | 58            | 56            |
| Diameter of the stem.. | —             | —             | 6             | 7             | 12            | 4             | 4             |

The thecal skeleton is composed of a great number of polygonal plates, the largest of which have a diameter of 7 mm. In the specimen figured in Pl. 7, fig. 8 [RM Ec 3276] the basal circlet probably contains 6 plates, whereas the specimen in Pl. 7, fig. 9 [RM Ec 2699] has at least twice this number. In the specimen last mentioned the stem is extremely wide.

The epithek is almost smooth with a very faint concentric ornament. An indication of an umbo is recognizable in some plates.

Where traceable, the pores of the thecal plates are seen to be connected by compound tangential canals, 2—4 of which extend between two pores. The separate tangential canals are fine and are densely set, so that there are on an average 7—8 in 1 mm. The pore-rhombs reach the plate-centre, even in cases where the y-axis of the rhomb is greater than the x-axis.

The ambulacral area, as mentioned, is not preserved in any specimen available. The peristomal projection broken off at its base is in RM Ec 3276 (Pl. 7, fig. 8) suboval in outline (great diam. 12 mm).

For reasons mentioned, the shape of the mouth is not known. The anus is pentagonal, being covered with a rather high pyramid of 5 valvules. In the said specimen its diameter is 10.5 mm.

The gonopore is subcircular, lying in the centre of a quadrangular swelling (cf. Pl. 7, fig. 8).

The lines o—g : g—a : a—o are in the average ratio 1 : 1.4 : 2.0.

The stem is not present in any specimen. As appears from the table of measurements above, it has in several instances been decidedly wider in relation to the width of the theca than in *Echinosphaerites aurantium* (N. B. especially the specimen in Pl. 7, fig. 9).

Discussion: — *Echinosphaerites grandis*, reported by JAEKEL (1899, p. 336) from the neighbourhood of Tallinna and from erratics in N. Germany, was not very well characterized, as pointed out. Therefore the identification of the Swedish material is only tentative, as well as the proposed synonymity between *E. grandis* and *E. pogrebowi* HECKER. The last-mentioned was described exhaustively by HECKER (1923, p. 35 seq.). A comparison reveals that our specimens agree fairly well with that form from strata in the Leningrad district (Kuckers) equivalent to the Lower Chasmops limestone in Sweden (cf. our Pl. 7, fig. 8 and HECKER 1923, Pl. 2, fig. 4). The Swedish specimens are as a rule somewhat larger than the Russian ones, but there is no very great difference in the character of the pore-system and the position of the "primary pores". According to measurements taken on HECKER's Pl. 2, fig. 4, the lines o—g : g—a : a—o are in the ratio 1 : 1.5 : 2.2. The aboral pole is possibly more projecting than in most of our specimens. Yet in specimens of smaller size [RM Ec 3271] this character is more pronounced. Since the Russian specimens are somewhat smaller than the main part of the specimens mentioned in the table of measurements above, the present writer does not attach any importance to the difference in shape.

HECKER's Pl. 2, fig. 3, shows a form designated as *Echinosphaerites* cf. *pogrebowi*. The specimen was derived from Ordovician strata in the island of Vaigach. The geologic horizon was given as equivalent to the Platyrus limestone in Sweden and thus older than the strata from where the rest of the fossil-material here discussed was obtained.

HECKER (1923, p. 36) brought up the idea that *Echinosphaerites grandis*, *E. pogrebowi* (these forms were provisionally not made identical), *E. difformis* JAEKEL, and *E. pirum* JAEKEL would prove not to be distinct but to display a closer mutual relationship. In the opinion of the present writer this form-complex probably is connected with *E. aurantium*.

Regional distribution: — Sweden, Östergötland: Fyrstensberget. — Dalarna: Kullberg. — ? Estonia. — ? USSR. — ? N. Germany (drift boulders).

Stratigraphic range: — Lower Chasmops limestone, Kullberg limestone, Upper Llandeilian (—Lower Caradocian?).

*Echinosphaerites* sp.

Pl. 8, fig. 6.

The specimen figured [RM Ec 3070] is a large pyriform theca, mainly exfoliated, on account of which the structure of the poresystem cannot be recognized. Yet it can be inferred from casts of the vertical pore-canals that the pore-rhombs extended to the plate-centre. The theca is imperfect in other respects, too. Thus i.a. the actinal region is destroyed. The theca measures 94 mm. in height and 71 mm in diameter. In another similar (imperfect) specimen [RM Ec 2755] the corresponding measurements are >80 mm and 67 mm. The greatest plates are about 7 mm in diameter.

With regard to the unsatisfactory state of preservation of the specimens, the writer has preferred to refer to them as *Echinosphaerites* sp. In size they exceed all other specimens examined by the author and in shape they are fairly well characterized. Yet it is possible that this form stands in the same relation to *Echinosphaerites grandis* JAEKEL ? as e.g. the specimen in Pl. 7, fig. 4, to the spheroidal forms of *E. aurantium*.

Among foreign species, *Echinosphaerites barrandei* JAEKEL [*Echinosphaerites* ("Arachnocystites") *infaustus* BARRANDE, ex parte] is comparable with our form in size and, to a certain degree, in shape of the theca. But they differ i.a. in the shape and extension of the pore-rhombs (cf. BARRANDE 1887, Pl. 22). The Bohemian species is from the stage d 4 of BARRANDE, which is equivalent to, or younger than, the Chasmops limestone, from where the Swedish specimen originates.

The specimen figured in Pl. 8, fig. 6, was collected in boulders on the west side of the Kinnekulle Mountain, Västergötland. Some smaller, less pyriform specimens from the same locality are possibly conspecific with the large specimen. The other large specimen referred to above is from the Billingen Mountain, Västergötland.

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Several finds of fragmentary or otherwise ill-preserved specimens from different provinces of Sweden have been referred to as "*Echinosphaerites* sp.". Thus by THORSLUND (1938), p. 28) from the 330.5—315.3 m level in the core from the deep-boring at File Haidar, Gotland. The horizon was determined as Lower Chasmops limestone.

Further, *Echinosphaerites* sp. was mentioned by THORSLUND (1940, p. 114) from boulders of Chasmops limestone at Tvären, Södermanland. The small fragment [RM Ec 2735] was examined by the present writer but is too imperfect to be determined closely.

In Lower Chasmops limestone at Åsarna, Jämtland, *Echinosphaerites* sp. is common in a certain horizon, according to THORSLUND (1940, p. 68). The same author (1940, p. 82) recorded *Echinosphaerites* sp. from the Upper



Chasmops series at Storgårdsbäcken, Jämtland. Further *Echinosphaerites* was listed without specific determination from the Kullberg limestone (THORSLUND 1936, p. 26).

In slabs of Staurocephalus shale (uppermost Ordovician) from Tommarp, Scania [LM], there are fossil-fragments designated by TROEDSSON (1918, p. 23) as anal-plates of *Echinosphaerites* sp. Obviously they were interpreted as valvules of anal pyramids. The present writer, after examining the fossils in question, is obliged to deny the interpretation given by TROEDSSON but can give no positive opinion of the nature of the fossils.

### *Echinosphaerites* ? sp.

Pl. 7, fig. 1,

1919 *Echinosphaerites aurantium* GYLLENH. — FUNKQUIST p. 38, Pl. 2, figs. 21—22.

The state of preservation of FUNKQUIST's specimens [LM] is too poor as to admit a safe specific, or even a generic, determination. Undoubtedly there is a certain similarity to *Echinosphaerites*. But the plates are larger by far than in the theca of any known species of *Echinosphaerites*.

The specimens are from Virrestad, Tommarp, and Tosterup, all in Scania. They originate from the so-called cystoid-shale in SE Scania, which may be supposed to represent Lower Chasmops beds, Upper Llandeilian.

## Order **Diploporita** J. MÜLLER 1854, emend. BATHER 1906.

The Diploporita were divided by JAEKEL (1918, p. 100 seq.) into three orders: — Asterocystida, Seriolata, and Sphaeronita. The present writer can see no reason not to accept the arrangement proposed by JAEKEL, only that the subdivisions will be taken as superfamilies. The first-mentioned of these is not represented in Sweden.

### Superfamily **Seriolata** JAEKEL 1918.

#### Family **Glyptosphaeritidae** (BATHER) BASSLER 1938.

BASSLER (1938, p. 12) referred to BATHER as author of the family "Glyptosphaeridae". Whether BATHER's paper of 1899 appeared earlier than JAEKEL's monograph published in the same year is not known by the present writer. If not, JAEKEL should stand as author of the conception, having in 1899 (p. 422) given a definition of the "Glyptosphaeridae".

Genus *Glyptosphaerites* MÜLLER 1854.Genotype: — *Sphaeronites leuchtenbergi* VOLBORTH 1846.Synonyms: — See ANGELIN 1878 a (p. 31) and JAEKEL 1899 (p. 423). Addendum: — *Protocrinus* (ex parte) EICHWALD 1856, 1860.Regional distribution: — USSR, Estonia, Sweden, ? Norway,<sup>1</sup> Germany (LORETZ 1884, p. 141; JAEKEL 1899, p. 425; FREYBERG 1923, p. 265), Bohemia (JAEKEL 1899, p. 425), Spain (JAEKEL 1899, p. 425).

Stratigraphic range: — Middle Ordovician (— ? Lower Silurian).

*Glyptosphaerites leuchtenbergi* (VOLBORTH 1846).

Pl. 9, figs. 2—6. Pl. 10, fig. 1. Text-fig. 18.

1840 *Sphaeronites pomum* WAHL. — EICHWALD, p. 201 (p. 189 of Germ. ed.).1843 *Sphaeronites pomum*, HIS. — LEUCHTENBERG, p. 23, Pl. 2, figs. 19—21.1846 *Sphaeronites Leuchtenbergi*, m. — VOLBORTH, p. 187, Pl. 10, figs. 1—7.1854 *Glyptosphaerites Leuchtenbergi*. — MÜLLER, p. 186.1856 *Protocrinus Leuchtenbergi* VOLB. [sic!]. — EICHWALD, p. 122.1860 *Protocrinus Leuchtenbergii* VOLB. — EICHWALD, p. 619.1878 *Glyptosphaera Leuchtenbergi* VOLBORTH. — ANGELIN 1878 a, Pl. 11, figs. 1—4.1896 *Glyptosphaera Leuchtenbergi*, JOH. MÜLLER [sic!]. — HAECKEL, p. 103, fig. 12.1899 *Glyptosphaerites Leuchtenbergi* v. VOLBORTH sp. — JAEKEL, p. 425, Pl. 4, figs. 3—6.1900 *Glyptosphaera Leuchtenbergi*. — BATHER, p. 73, fig. 43.

Holotype: — The specimen figured in VOLBORTH 1846, Pl. 10, fig. 1; present depository unknown to the writer.

Type locality: — Unknown (USSR; probably Pavlovsk or Pul'kova).

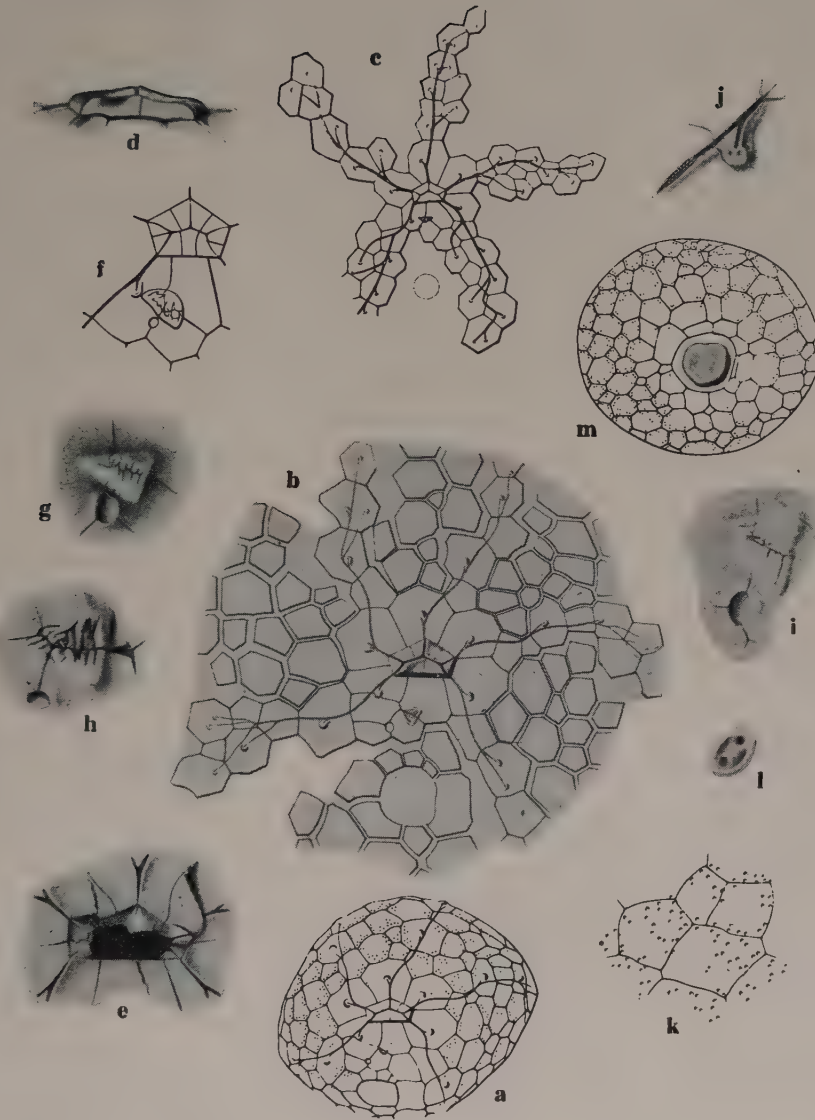
Type stratum: — Unknown.

Material: — 38 specimens [RM, SGU], some of which are rather well-preserved.

Remarks: — Since the Swedish material of this species agrees perfectly — as far as the writer is aware — with specimens from the East Baltic area described exhaustively by LEUCHTENBERG (1843), VOLBORTH (1846), JAEKEL (1899), and BATHER (1900), a full description is not needed here. Referring to the papers mentioned, our plate-figures, and text-fig. 18 displaying several details of the organization, the author restricts himself to some comments on the material available.

The thecae are spheroidal or somewhat flattened from the poles. Their diameter varies between 20 and 54 mm.

<sup>1</sup> *Glyptosphaerites* is not reported from Norway in literature. In the author's opinion a poorly preserved thecal fragment [RM Ec 5175] from the Oslo-region, labelled Baad-bugten, belongs there.



Text-fig. 18. *Glyptosphaerites leuchtenbergi* (VOLBORTH) (drawn from Russian specimens in the then Imp. Academy of Sciences of St. Petersburg). a Specimen in oral view. b Ventral half of the theca projected from the oral pole. c The ambulacral system and supporting thecal plates. d The mouth in lateral view. e The mouth with OO removed. f The postero-oral region. g—i Madreporite and gonopore. j Detail of ambulacral groove showing covering plates and a brachiole-facet. k Part of the thecal skeleton. l A diplopore within its peripore. m Specimen in basal view. (From LOVÉN MS, Pl. 5; lettering by the present writer. About  $\frac{2}{3}$  of original size.)

The pores, within their peripores, in many cases are concentrated to the upper part of the plates (Pl. 10, fig. 1), as illustrated by LEUCHTENBERG (1843, Pl. 2, fig. 20) already. But in several instances the pores are seen to be distributed more irregularly all over the plates, as in the figures communicated by JAEKEL (1899, Pl. 4, figs. 3—5). It is noticeable that the diplopores are not seldom sectioned by the sutures.

The madreporite, well illustrated in text-fig. 18, is not perfectly preserved in any specimen available.

Minute side-plates and covering plates of the ambulacra are recognizable in certain specimens (Pl. 9, fig. 3). One thecal plate bears as a rule one brachiole-facet only (Pl. 9, fig. 4), but in some cases there are two (Pl. 9, fig. 5) or even three [RM Ec 4181].

The stem is not preserved in any specimen.

The occurrence of this species in Ordovician deposits of Sweden was observed by JAEKEL (1899, p. 425).

**Regional distribution:** — Sweden, Öland: Hulterstad, Löt (boulders). — Östergötland (closer locality unknown). — Dalarna (closer locality unknown; 2 specimens [SGU] that cannot be determined safely are from Kårgårde). — Stockholm (boulders, probably from the N. Baltic area). — Estonia. — USSR.

**Stratigraphic range:** — The species has an unusually wide stratigraphic range. In the East Baltic area it appears in the Vaginatum limestone, B<sub>3</sub> (EICHWALD 1860, p. 620; SCUPIN 1928, p. 172). Further it occurs in the Aseri stage ("Echinosphaerites zone"), seems not to have been met with in the Lasnamäe ("Baukalkstein") but re-appears in the Uhaku ("Caryocystites zone") (ORVIKU 1927 a, pp. 15, 22). This corresponds to the space Upper Arenigian—Middle Llandeilian of the British time-table. All specimens from Öland are from the zone of *Asaphus platyurus*, which is an equivalent of the Aseri. The material from Östergötland is labelled very imperfectly. No horizon is given, but judging from the rock (a reddish grey limestone) it can have been collected from the zone of *Megalaspis gigas*, which falls between the Vaginatum limestone and the Aseri.<sup>2</sup> The specimen from Dalarna (the two dubious specimens are not considered) is from "Upper red Orthoceratite limestone" (=the zones of *Megalaspis gigas* and *Asaphus platyurus*).

<sup>2</sup> In Östergötland there is a considerable break in the series of strata, comprising the upper part of the Asaphus series. It is possible that this hiatus begins with the zone of *Megalaspis gigas* already. If this be the case, our specimen must have been derived from the Asaphus limestone (=the Vaginatum limestone in Estonia). Red limestone belonging to this zone was reported from several localities in the province by LINNARSSON & TULLBERG (1882, p. 24).



*Glyptosphaerites suecicus* (ANGELIN 1878).

Pl. 9, fig. 1.

1878 *Glyptosphaera suecica* ANG. — ANGELIN 1878 a, p. 31, Pl. 11, figs. 5—6.1888 *Glyptosphaera suecica* A. — LINDSTRÖM 1888 a, p. 23.

Holotype: — RM Ec 2377.

Type locality: — Unknown (Dalarna).

Type stratum: — Unknown ("Leptaena limestone", according to LINDSTRÖM 1888 a, p. 23).

Material: — The holotype and one other specimen possibly referable to this species.

Remarks: — This species is founded on a specimen that is in several respects very imperfect. The clear figures given by ANGELIN (1878 a, Pl. 11, figs. 5—6) are very remote from representing the actual specimen. The whole theca is weathered and worn, a good deal of the test is wanting, and the development of the elements of the ambulacral system is not distinctly recognizable. The proximal portion of the stem indicated in ANGELIN's fig. 5 is not present. The height of the theca is 26 mm and the greatest diameter 29 mm.

The short description given by ANGELIN (1878 a, p. 31) runs as follows (here translated from the Latin): "Theca small, with pores radiating from the plate-centres". It contains hardly anything of diagnostic importance suited to distinguish this form from *Glyptosphaerites leuchtenbergi*. The smallest specimens in hand of the species mentioned do not reach the size of *G. suecicus*. Further, as we have seen, the pores are not always concentrated in the upper part of the plates but are sometimes distributed all over the plate-surface much in the same way as in the form under discussion. In consequence of the poor state of preservation of *Glyptosphaerites suecicus*, moreover, we cannot state safely that the arrangement of the pores proposed by ANGELIN has been characteristic of all plates, even if recognizable in some of them.

The ambulacra, as far as traceable, show no obvious difference from those of *Glyptosphaerites leuchtenbergi*.

In consideration of the facts here emphasized one cannot help wondering if ANGELIN's form is specifically distinguished from *Glyptosphaerites leuchtenbergi*. With regard to the scanty material available of *G. suecicus*, the writer is not prepared to give a definite answer to the question. Since its geologic horizon is uncertain but possibly is above — maybe considerably above — the upper limit of the known stratigraphic range of *G. leuchtenbergi* in the East Baltic area, caution bids us not simply to disqualify ANGELIN's species but to retain it provisionally.

The second specimen [RM Ec 2368] tentatively referred here is minor

than the holotype (height of the theca 21.5 mm) and is still more poorly preserved. Strictly, it is hardly specifically determinable; it was not taken along with *Glyptosphaerites leuchtenbergi* because it originates from as high a geologic horizon as the Lower Chasmops limestone ("Cystoid-limestone", according to the label).

**Regional distribution:** — Sweden, Dalarna. The locality of the holotype is not known, whereas the second specimen is from Åberga.

**Stratigraphic range:** — Not known with certainty. The holotype, as mentioned above, was proposed to have been derived from the so-called Leptaena limestone. Reef-limestones (Kullberg and Boda limestones) included in this conception were formed at different periods in the time-space Middle Ordovician—Lower Silurian. The oldest part of the Kullberg limestone is equivalent to part of the Lower Chasmops limestone, from where the second specimen available is said to have been collected.

#### Family **Gomphocystitidae** (BATHER) BASSLER 1938.

##### Genus **Gomphocystites** HALL 1864.

**Genotype:** — *Gomphocystites glans* HALL 1864.<sup>3</sup>

**Synonymy:** — *Gomphocystis* auctorum.

**Diagnosis:** — A genus of Gomphocystitidae with pyriform or helmet-shaped theca; ambulacra long, extending spirally over the theca in solar direction; plates in radial and interradial zones; gonopore and anus close to the mouth.

**Regional distribution:** — N. America, Sweden.

**Stratigraphic range:** — Middle Silurian.

##### **Gomphocystites gotlandicus** (ANGELIN 1878).

Pl. 10, figs. 2—4.

1878 *Gomphocystis gotlandica* ANG. — ANGELIN 1878 a, p. 31, Pl. 9, fig. 20.

1888 *Gomphocystis gotlandica* ANG. — LINDSTRÖM 1888 b, p. 20.

1899 *Gomphocystites gotlandicus* ANGELIN. — JAEKEL, p. 421, Pl. 2, fig. 10.

**Holotype:** — RM Ec 5077, a very worn and imperfect specimen.

**Type locality:** — Lansa, Fårö.

**Type stratum:** — Höglint limestone, Middle Silurian.

<sup>3</sup> FOERSTE (1920 b, p. 59) proposed *Gomphocystites tenax* HALL 1864 to be the genotype. Yet *Gomphocystites glans* had earlier been appointed to that dignity (MILLER 1889, p. 249).

**Material:** — Some 75 specimens [RM], most of them very fragmentary.

**Diagnosis:** — A species of *Gomphocystites* with helmet-shaped theca (the dorsal portion wanting?) with very narrow ambulacra, each ambulacrum being supported by a single series of plates; between these radial plates there is, in point of principle, one single row of plates often elongated perpendicularly to the ambulacra; interradial and — though less regularly — radial plates strongly papillose.

**Description:** — The general shape of the theca may be said to recall approximately that of a helmet. But the basal surface is not exposed in any specimen, so it is possible that the dorsal portion of the theca has been produced into a stem, in agreement with the American species. In many specimens the theca is somewhat compressed from the sides, having thus an oval transverse section, which seems to be a secondary feature, however.

**Measurements.** The holotype has a diameter of about 20 mm. In other specimens it varies between 15 and about 30 mm. In the specimen to the right in Pl. 10, fig. 4, the height is 13 mm at a diameter of 18 mm.

**Thecal skeleton.** The theca is composed of a great number of irregularly polygonal plates. Thanks to the extension of the ambulacra, radial and interradial zones are recognizable, each of them, in point of principle, consisting of one row of plates only. But there are frequent anomalies in this plan, caused by coalescence between radial and interradial plates or by irregular dividing of the plates in the interradial zones. Roughly the plates are disposed in 10 zones in spiral arrangement, however. The radial plates, in which the ambulacral grooves are incised, are as a rule more or less quadrangular in outline, whereas the interradial plates often are elongated in a direction perpendicular to the ambulacra. The structure of the skeleton can be well studied in the specimens RM Ec 5101 and 5106. — The thickness of the test amounts to 3 mm.

**Surface structures of stereom.** The thecal plates, and especially those of the interradial zones, are strongly papillose. The papillae vary considerably in shape. Now they are mamillary, now produced into veritable spines, now they are plate-shaped owing to coalescence between several papillae.

**Pores of the thecal plates.** Typical diplopores are present, as best seen in abraded specimens or in internal view (Pl. 10, fig. 3). The pores are very small and densely set within the peripore. In one plate there can be as many as 10—12 diplopores, but usually there are some few only. They open all over the theca, even in the papillae.

**Ambulacral system.** The five ambulacra extend in spiral over the theca, curving in solar direction. Their course could not be followed in

detail in lack of a perfect specimen. At their origin the ambulacra in the radii I and II as well as in IV and V have a common stem, which divides in the immediate neighbourhood of the mouth. The ambulacrum of radius III originates from the anterior side of the mouth. — JAEKEL (1899, p. 420; Pl. 2, fig. 10) described and illustrated how short side-branches set out to the left of the ambulacra. These side-branches, if present at all, are merely indicated in all specimens examined by the writer. Nor is there any trace of facets for the numerous brachioles announced by JAEKEL. It is remarkable that FOERSTE (1920 b, p. 56 seq.) could state positively the absence of brachiole-facets in *Gomphocystites indianensis* MILLER and in an unnamed species of *Gomphocystites*. About the first-mentioned he wrote: — "Along the sides of the food-grooves there are depressions or grooves which may locate the sutures between the bordering plates. If they represent branches of the food-grooves, then it should be observed that they lead to no facets for brachioles. Parts of the surface are so well preserved that the absence of any evidence of the presence of brachioles should be emphasized." In *Gomphocystites bownockeri* there are small brachiole-facets, however. — No covering plates of the ambulacra were observed.

According to JAEKEL, a hydropore is not developed. Nor could the present writer ascertain any.

**Alimentary canal.** The mouth is oval or subcircular. It is very small, having in well-preserved specimens a diameter of about 1 mm only. The anus, separated from the mouth by 1 plate, is circular. Its diameter is about twice that of the mouth. The anus lies in interradius V—I. Covering plates of mouth or anus were not stated.

The gonopore is a very small circular aperture immediately above the anus and somewhat in solar direction of it.

The basal termination, as mentioned, is not visible in any specimen available.

**Remarks:** — *Gomphocystites gotlandicus* is the only representative in Europe of its genus, all other species are N. American. Three species (*G. tenax*, *G. glans*, *G. clavus*)<sup>4</sup> were described in 1864 by HALL and a fourth species, *Gomphocystites indianensis*, by MILLER 1889. FOERSTE (1920 b) announced a new species, *G. bownockeri*, and a form not specifically determined. These are all species made known to science.

The Gotland species is well characterized by the shape of the theca and the strong development of the papillae on the thecal plates. Further mouth and anus are smaller than in the other species, and the ambulacra seem to be fainter.

<sup>4</sup> *Gomphocystites clavus* was identified tentatively with *G. glans* by JAEKEL (1899, p. 421). But it was regarded as a separate species by MILLER (1889, p. 249), BASSLER (1915, p. 561), and FOERSTE (1920 b, p. 59).



**Regional distribution:** — Sweden, Gotland: Hangvar, Kappelshamn, Lansa (Fårö), Stenkumla.

**Stratigraphic range:** — Höglint group, lower part of Wenlockian.<sup>5</sup> The horizon was kindly confirmed by Dr HEDE.

## Superfamily *Sphaeronitida* (JAEKEL 1918) n. nomen.

### Family *Sphaeronitidae* NEUMAYR 1889.

#### Genus *Sphaeronites* HISINGER 1828.

**Genotype:** — *Echinus pomum* GYLLENHAAL 1772.

**Synonyms:** — See ANGELIN 1878 a (p. 30) and BASSLER 1938 (p. 172).

**Diagnosis:** — A genus of *Sphaeronitidae* with more or less rounded theca, attached directly with the basal surface, or slightly tapering in basal direction; theca composed of a great number of plates pierced by numerous diplopores within suboval or polygonal peripores with more or less raised margins; the individual ambulacra not branching fan-like; anus close to the mouth; gonopore at the upper left side of the anus.

**Remarks:** — In all older papers the genus *Haplosphaeronis* JAEKEL 1926 is included in *Sphaeronites*. The removing of the genus mentioned has necessitated a revision in some points of the diagnosis of *Sphaeronites*.

**Regional distribution:** — Sweden, Norway (KJERULF 1865, p. 4; BRÖGGER 1882, p. 42; KLÆR 1897, p. 17), Yunnan (REED 1917, p. 12; 1936, p. 13; YIN & LU 1936—1937, pp. 47, 53).<sup>6</sup>

**Stratigraphic range:** — Middle Ordovician.

#### *Sphaeronites pomum* (GYLLENHAAL 1772).

Pl. 1, figs. 2, 3, 5. Pl. 11, figs. 6—9, 12. Pl. 12, figs. 2, 4, 6. Pl. 13, fig. 2.

Text-figs. 1: 1—3; 19: 1—3, 7—9; 20—21.

1772 *Echinus Pomum*. — GYLLENHAAL, p. 253, Pl. 8, figs. 1—3.

1818 *Echinosph. Pomum*. — WAHLENBERG, p. 49.

1821 *Echinospaerites Pomum*. — WAHLENBERG, p. 54.

<sup>5</sup> Cf. HEDE, J. E., 1942. On the correlation of the Silurian of Gotland. — Lunds Geol. Fältklubb 1892—1942. (Medd. Lunds Geol.-Min. Inst. **101**). Lund. P. 14.

<sup>6</sup> It is possible that *Sphaeronites* is represented in Great Britain also. MÜLLER (1854, pp. 186—187) suggested that certain forms described by FORBES (1848) as *Caryocystites* are rather *Diploporita* related to *Sphaeronites pomum*. One of the forms alluded to was described by REED (1897, p. 82) under the name of *Sphaeronites pyriformis* (FORBES). Judging from the description, the species in question hardly belongs to *Sphaeronites* as conceived here.

- 1826 *Echinosphaerites pomum*. — SCHLOTHEIM, column 313, Pl. 1, fig. 5 a [non 5 b].  
 1828 *Sphaeronites Pomum*. — DALMAN, p. 133, foot-note 1.  
 1837 *Sphaeronites Pomum*. — HISINGER 1837 b, p. 91, Pl. 25, fig. 7 [cop. from GYLLENHAAL 1772].  
 1840 *Sphaeronites Pomum*. — BUCH, p. 58.  
 1878 *Sphaeronis pomum* GYLLENH. — ANGELIN 1878 a, p. 30, Pl. 11, figs. 11—12; Pl. 27, figs. 14—16; Pl. 28, figs. 10, 10 a, 10 b.  
 1888 *Sphaeronis pomum* GYLLENH. — LINDSTRÖM 1888 a, p. 10.  
 1896 *Sphaeronites pomum*, HISINGER, 1837 [sic!]. — HAECKEL, p. 98.  
 1899 *Sphaeronites pomum* GYLLENHAAL 1772 sp. — JAEKEL, p. 398.<sup>7</sup>

[Non *Echinus pomum* HISINGER 1802, p. 189 (= *Sphaeronites globulus* (ANGELIN)). — Non *Sphaeronites pomum* HISINGER 1828, pp. 196—197, Pl. 5, figs. 2—4 (figs. 2—3 = *Echinosphaerites aurantium* (GYLLENHAAL); fig. 4 = *Sphaeronites globulus*). — Non *Echinosphaerites Pomum*? KLÖDEN 1834, p. 243 (see p. 11, foot-note 10 above). — Non *Sphaeronites pomum* EICHWALD 1840, p. 201 (= *Glyptosphaerites leuchtenbergi* (VOLBORTH)). — Non *Sphaeronites pomum* LEUCHTENBERG 1843, p. 7 (as the preceding). — Non *Echinosphaerites pomum* VERNEUIL 1845, p. 24, Pl. 1, fig. 7 (= *Protocrinites oviformis* EICHWALD). — Non *Sphaeronites Pomum* BUCH 1846 a, p. 104 (= *Sphaeronites globulus*, fide JAEKEL 1899, p. 398). — Non *Sphaeronites pomum* BUCH 1846 c, p. 31 (as the preceding). — Non *Sphaeronites pomum* MÜLLER 1854, p. 186 (as the preceding). — Non *Sphaeronites pomum* EICHWALD 1856, p. 122 (= ? *Glyptosphaerites leuchtenbergi*). — Non *Sphaeronites* (*Echinus*) *pomum* EICHWALD, p. 617, Pl. 32, figs. 9—10 (fig. 9 = ?; fig. 10 = *Bockia* sp., fide HECKER 1938 a, p. 68). — Non *Echinosphaerites pomum* var. KJERULF 1865, p. 4 (= *Sphaeronites globulus* var., fide BRÖGGER 1882, p. 42, foot-note 1). — Non *Sphaeronites pomum* LOVÉN 1867, p. 438, fig. 5 (= *Sphaeronites globulus*). — Non *Sphaeronites pomum* LOVÉN 1868, p. 180, fig. 5 (as the preceding).]

A number of quotations of the species in faunal lists &c. were not considered at compiling the list of synonyms.

Neotype: — RM Ec 2781.

According to kind information by Dr N. ZENZÉN, GYLLENHAAL's original specimens probably are lost (cf. p. 4, foot-note 5). Yet, as pointed out on p. 141 above, it is not quite out of the question that some specimen from GYLLENHAAL's collection will be discovered. Therefore the neotype here appointed may be looked upon as provisional. The specimen chosen is the original of Pl. 11, figs. 11—12 in ANGELIN 1878 a. The specimen is not perfect since the actinal region with the oro-anal area is damaged. But the test ist partially well-preserved. The neotype — from the Kinnekulle Mountain in Västergötland — is rather likely to represent a topotypical specimen. It

<sup>7</sup> Pl. 4, fig. 9, in JAEKEL 1899, according to the explanation of the fig. represents *Sphaeronites pomum*, whereas in the text (p. 398) it is referred to *Sphaeronites globulus*. Since the covering plates of mouth and anus are preserved, which is not the case in any specimen of *Sphaeronites pomum* examined by the writer, it may be assumed that the fig. represents *Sphaeronites globulus*. It is true that the specimen from which the fig. was drawn was proposed to have been derived from "grey Orthoceratite limestone". Very likely no importance can be attached to this proposal, however.

is true that GYLLENHAAL knew the species from several areas of Sweden, but Kinnekulle was mentioned first.

**Type locality:** — Not known (cf. above; loc. of the neotype: — Kinnekulle, Västergötland).

**Type stratum:** — Asaphus limestone, Middle Ordovician.

**Material:** — A rather extensive material (approximately 500 specimens) was available to the writer. Several specimens are in a fairly good state of preservation. The species is represented in the HISINGER and WAHLENBERG collections.

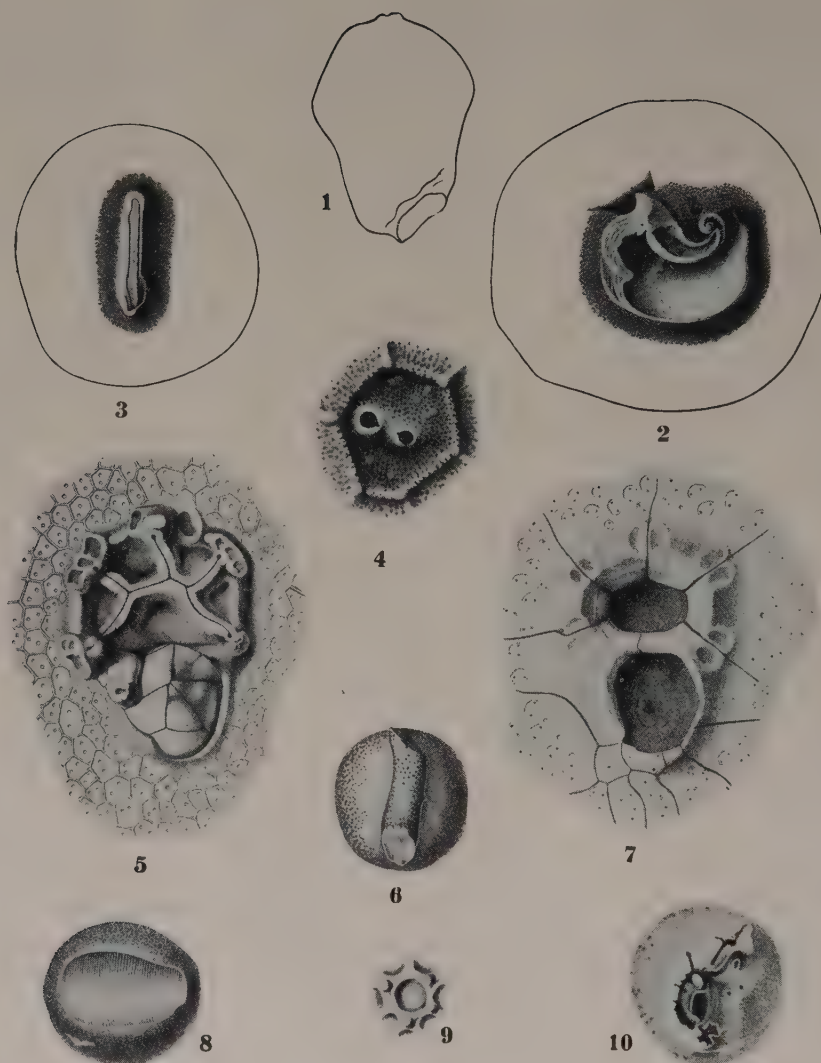
**Diagnosis:** — A species of *Sphaeronites* with spheroidal theca (in typical forms), sessile on a broad base; pores usually not present in a marginal zone of the thecal plates; the surface of the test has a rough appearance, owing to the strong development of the walls of the peripores; where these walls meet they form knots or veritable blunt spines.

**Description:** — General shape of the theca. In most specimens the theca is spheroidal. Yet it varies rather considerably in shape, as appears from Pl. 11, figs. 6—9. In certain specimens the height of the theca is greater than the width, in others the width is greater than the height. The elongated theca of the specimen figured in text-fig. 19: 1 must be considered as an anomaly. On examining the specimen one gets the impression, moreover, that it has been crushed and deformed.

**Measurements.** The thecae vary in size between about 10 mm and about 45 mm. The bulk of the specimen have a diameter of 30—35 mm. Yet it should be noted that in the material from Västergötland the size-order below 20 mm is represented by numerous specimens. The lectotype is relatively small, its greatest diameter being 28 mm and the height about the same.

**Thecal skeleton.** The theca is composed of an indefinite number of polygonal plates, presumably amounting to several hundreds. As a rule the sutures are not visible but may be traced by the zones devoid of thecal pores bordering the plates. In many cases the plates are somewhat vaulted, which also contributes to bring out the outline of the plates (Pl. 11, figs. 6, 8. Pl. 12, fig. 2 b). The plates may attain a size of 6 mm but are usually smaller. In outline they vary a good deal. Some plates are triangular whereas others have eight (or maybe still more) sides. The thickness of the test varies a good deal as appears from a comparison of Pl. 1, fig. 2, with Pl. 13, fig. 2. In the specimen in the last-mentioned fig. the test forms a heavy armour with a thickness of more than 1 mm.

**Pores of the thecal plates.** Each plate is pierced by a great many diplopores, the number of which stands of course in relation to the size of the individual plates. In a large plate there are 50—60 diplopores. These are surrounded by subcircular or polygonal peripores, the walls of which flow together forming a coherent network elevated over the surface



Text-fig. 19. 1. *Sphaeronites pomum* (GYLLENHAAL), outline of an anomalous specimen [RM Ec 4186]; about  $\frac{2}{3}$  of nat. size. Böda(?), Öland. 2. The same species, showing the basal surface of a specimen which was attached to the shell of a gastropod [RM Ec 4187]; somewhat magnified; the same loc. 3. The same species [RM Ec 4188], showing the basal surface of a specimen growing around a shell-fragment; about  $\times 1.5$ ; the same loc. 4. *Sphaeronites globulus* (ANGELIN) [RM Ec 4193], diplopore; about  $\times 20$ . Böda, Öland. 5. The same specimen, ambulacral and anal area;  $\times 5$ . 6. *Haplosphaeronis* sp. [RM Ec 115], showing the basal surface of a specimen attached to a coral or bryozoan stock; about  $\times 2$ . Fjäckå, Dalarna. 7. *Sphaeronites pomum* (GYLLENHAAL) [RM Ec 4189], as fig. 5, covering plates removed; about  $\times 6.5$ . Böda(?), Öland. 8. The same species, showing the basal surface of a specimen which was attached to the shell of an orthoceratite [RM Ec 4190]. 9. The same specimen as in fig. 7?, detail of a weathered portion of the thecal wall; about  $\times 14$ . 10. *Eucystis* sp., basal surface;  $\times 2$ . Arvet, Dalarna. (From LOVÉN MS, Pl. 9; original numbering retained. About  $\frac{2}{3}$  of original size.)



of the plates. At the angles the walls are raised so as to form knobs or short spines (see especially the thin-section, Pl. 12, fig. 6, and text-fig. 19: 9). It was mentioned already that the marginal zones of the plates often are devoid of pores. The pore-canals are largely perpendicular to the surface of the theca (cf. Pl. 13, fig. 2).

The *ambulacral system* is concentrated in the immediate neighbourhood of the mouth and in close connexion with the periproct. The whole of the oro-anal area forms a subtriangular stereometric swelling (Pl. 11, fig. 12, Pl. 12, fig. 4, Text-fig. 19: 7). There are 5 very short *ambulacra*. In most cases the state of preservation does not admit of making out details in the structure of the ambulacral area, but it is likely that the normal number of *brachiole-facets* is 5. JAEKEL (1899, p. 398) stated the number of brachioles to be 10 in *Sphaeronites pomum* as well as in *Sphaeronites globulus*. A *hydropore* has not been observed.

*Alimentary canal.* The mouth is pentagonal and elongated in transverse direction. The anus is rounded or oval, having its long axis perpendicularly to that of the mouth. The two apertures are often fairly equal-sized, with a diameter of about 1.5 mm.

A *gonopore* was not recognized.

The basal portion of the theca is generally broad. Very often the theca is attached directly with its lower surface to some foreign organism, the shell of which is not seldom found still in connexion with the theca. Thus it is evident that the lectotype was attached to the carapace of a trilobite. In many cases the shell of an orthoceratite served as substratum (text-fig. 19: 8). It may be supposed that specimens attached to the striated shell of an orthoceratite caused JAEKEL (1899, pp. 348, 349, 396) to suggest an epiphytic mode of life for *Sphaeronites*. For he advanced the opinion that the thecae were attached to plants or pieces of wood. The hypothesis must be said to be improbable throughout. — Text-fig. 19: 2 shows the lower surface of a theca attached to the shell of a gastropod. In text-fig. 19: 3 another mode of attachment is demonstrated. Here the basal surface of the theca has grown around an edge-wise erected shell-fragment.

*Discussion:* — In the same manner as *Echinospaerites aurantium*, this species acts as a rock-forming organism. *Sphaeronites*-beds are known from Öland and Västergötland. In the first-mentioned district the *Sphaeronites*-bearing horizon can be followed for a distance of more than 70 km (HADDING 1933, p. 51). In Västergötland the *Sphaeronites*-horizon is well developed in the Kinnekulle Mountain. WESTERGÅRD (1928, p. 45) remarked that it is likely to be present in Billingen also. This is confirmed by a slab with crowded specimens from Karlsfors [LM]. At a short visit to Österplana (Kinnekulle) the author made the following observations concerning the appearance of *Sphaeronites*-associations in an old quarry near the church: —



Text-fig. 20. Section through the *Sphaeronites pomum*-bearing strata (Asaphus limestone) in an old quarry near the church of Österplana on the Kinnekulle Mountain, Västergötland. The hand points at the main bed at the boundary between grey (Lower Asaphus) and red (Upper Asaphus) limestone. — Phot. A. HADDING 1943.

A strongly marked bed replete with *Sphaeronites* is found at the boundary between grey (Lower Asaphus) and red (Upper Asaphus) limestone. About 20 cm below this bed there is another *Sphaeronites*-horizon, in which the specimens regularly are of smaller size. Between the two beds scattered specimens occur, as well as below the lower *Sphaeronites*-horizon. It could be suspected that more than one species of *Sphaeronites* is represented in this section, since there is a clear difference in size between specimens in the lower and the upper horizon. But there are all sorts of intermediate forms between the two extreme types, and there is no obvious difference in the structure of the test, should it not be that the surface seems to be smoother in the small specimens. But the specimens are as a rule very poorly preserved. Anyhow, it is evident that *Sphaeronites pomum* in typical development was preceded by a smaller form which must be regarded as conspecific, however. Since there are no really distinguishing features, and variations in size are too vague as to be used for diagnostic purposes, there is no reason to denote the smaller specimens by a separate name. Yet we have to recognize that *Sphaeronites pomum* is a complex species. In fact it was proposed by HOLM (1901, p. 47) and WESTERGÅRD (1943, p. 68) that several species of *Sphaeronites* occur in the so-called "täljstenen" (=Lower Asaphus limestone) in Västergötland. A similar proposal was made by MÖBERG (1890, pp. 13—14) on discussing the *Sphaeronites*-bed in Öland. In this area smaller specimens were said to occur above the main horizon.

The *Sphaeronites*-bed is not known from other Ordovician areas of Sweden, as far as appears from literature. With regard to the large material of *Sphaeronites pomum* from Östergötland (especially Kungs Norrby) there

Text-fig. 21. The surface of the *Sphaeronites*-bed between the Lower and the Upper *Asaphus* limestones at the locality mentioned in the explanation of text-fig. 20. — Phot. A. HADDING 1943.



is yet reason to assume that it is rock-forming in this province too. The author is not aware when the material [in RM] was collected. It seems to have been relatively recently, for in 1884 TÖRNQUIST (p. 686) declared that the *Sphaeronites*-bed is lacking not only in Dalarna but also in Östergötland. Much earlier DALMAN (1828, p. 133) had stated that *Sphaeronites pomum* is not met with in Östergötland. — In Dalarna the *Sphaeronites*-bed is definitely not developed (LINNARSSON 1871 b, p. 343, foot-note 1; TÖRNQUIST 1884, p. 686), nor in Scania, as observed already by WAHLENBERG (1821, p. 53).

The specific differences between *Sphaeronites pomum* and the younger *Sphaeronites globulus* appear from the diagnoses given for these species. It is noticeable (as pointed out above, p. 162, foot-note 7) that the covering plates of mouth and anus are not preserved in any specimen of the former species but almost invariably in the latter. — The East Asiatic species described by REED (1917) are remote from the Swedish forms.

Regional distribution: — Västergötland: Kinnekulle (the following localities are verified by museum specimens: Gössäter, Lukastorp, Mörkelund, Råbäck, Trolmen, Verlaskog, Västerplana, Österplana), Billingen (Karlsfors, Ulunda), Mösseberg (Ranten), Älleberg. — Östergötland: Borghamn, Kungs Norrby, Skarpåsen. — Öland: Böda (not Böda Harbour), Lopperstad, Resmo, Smedby.<sup>8</sup> — Dalarna [some few specimens, RM Ec 2338, 2341, 2342, 2344, 2345, from an unknown locality]. — Jämtland: Högbro

<sup>8</sup> Material from Öland is very poorly represented in the collections available to the writer. Undoubtedly this is due to the bad state of preservation of the fossils which does not prompt collectors to turn their attention to them.



at Hårkan [WAHLENBERG collection, UM ec 1500, 1501]. — Skåne: Fågelsång [2 specimens, RM Ec 5025, 5026].<sup>9</sup>

Stratigraphic range: — Asaphus limestone, Upper Arenigian.

Investigations in Öland carried out by MOBERG (1890, p. 13) proved that the *Sphaeronites*-bed is an excellent guide-horizon of the upper part of the Lower Asaphus limestone. It forms the boundary towards the Upper Asaphus limestone. Yet, as remarked MOBERG (1890, p. 13) and as the writer has had occasion to confirm, *Sphaeronites* occurs also in the red Upper Asaphus limestone, although chiefly in scattered specimens.

### *Sphaeronites globulus* (ANGELIN 1878).

Pl. 11, figs. 10—11. Pl. 12, figs. 1, 3, 5. Pl. 13, fig. 1. Text-fig. 19: 4—5.

1802 *Echinus pomum*. — HISINGER, p. 189.

1828 *Sphaeronites pomum* (ex parte). — HISINGER, pp. 196—197, Pl. 5, fig. 4.

1846 *Sphaeronites pomum* HIS. [sic!]. — BUCH 1846 a, p. 104, fide JAEKEL 1899, p. 398.

1846 *Sphaeronites pomum*, HISINGER [sic!]. — BUCH 1846 c, p. 31, fide JAEKEL 1899, p. 398.

1854 *Sphaeronites pomum* HIS. [sic!]. — MÜLLER, p. 186, fide JAEKEL 1899, p. 398.

1867 *Sphaeronites pomum* GYLLENHAHL. — LOVÉN, p. 438, fig. 5.

1868 *Sphaeronites pomum* GYLL. — LOVÉN, p. 180, fig. 5.<sup>10</sup>

1878 *Sphaeronites globulus* ANG. — ANGELIN 1878 a, p. 30, Pl. 11, figs. 7—10.

1878 *Sphaeronites ovalis* ANG. — ANGELIN 1878 a, p. 30, Pl. 11, figs. 13—16.

1888 *Sphaeronites globulus* A. — LINDSTRÖM 1888 a, p. 16.

1896 *Sphaeronites globulus*, ANGELIN. — HAECKEL 1896, p. 98.

1896 *Sphaeronites ovalis*, ANGELIN. — HAECKEL 1896, p. 98.

1899 *Sphaeronites globulus* ANGELIN. — JAEKEL, p. 398, Pl. 4, fig. 9.<sup>11</sup>

1900 *Sphaeronites pomum* (ex parte). — BATHER, p. 72, fig. 39.

Holotype: — RM Ec 4360.

Type locality: — Böda Harbour, Öland.

Type stratum: Lower Chasmops limestone, Middle Ordovician.

Material: — About 150 specimens [LM, RM], by far the greatest part of which is from Öland. Some specimens in the HISINGER collection belong to this species.

Diagnosis: — A species of *Sphaeronites* with spheroidal or ovoid theca, generally tapering into a basal portion with the shape of a wide and

<sup>9</sup> The discovery of *Sphaeronites pomum* (in one sample associated with *Ampyx volborthi* F. SCHMIDT) at Fågelsång implies that the Orhoceratite limestone here reaches as high a stratigraphic horizon as the Lower Asaphus limestone.

<sup>10</sup> The reasoning displayed in foot-note 7 (p. 162 above) in the case of a fig. in JAEKEL 1899 is valid for the fig. 5 in LOVÉN 1867 and 1868, too. As far as the writer is aware it cannot be doubted that LOVÉN's fig. refers to *Sphaeronites globulus*. The fig. is reproduced in BATHER 1900, p. 72, fig. 39.

<sup>11</sup> Cf. above p. 162, foot-note 7.



short stem; pores distributed all over the plates; the surface of the test smooth upon the whole, the walls of the peripores forming no knobs or spines.

**Description:** — General shape of the theca. The theca is spheroidal or ovoid, the last-mentioned shape being more characteristic of this species than of *Sphaeronites pomum*. The basal portion of the theca often tapers into a wide, stem-like prolongation.

| (Measurements in mm)   | RM Ec<br>4647 | RM Ec<br>4193 | RM Ec<br>4465 | RM Ec<br>118 | RM Ec<br>4360<br>(holotype) | RM Ec<br>4336 | RM Ec<br>4303 | RM Ec<br>4432 |
|------------------------|---------------|---------------|---------------|--------------|-----------------------------|---------------|---------------|---------------|
| Height of the theca .. | 34            | 34            | 33.5          | 30.5         | 27                          | 21            | 19            | 15            |
| Greatest diameter .... | 34            | 30            | 31            | 26           | 25                          | 21            | 18            | 15            |

**Thecal skeleton.** The theca is composed of a great number of polygonal plates. They were counted in some specimens. Thus in RM Ec 4465, which is a large one (cf. the table of measurements above), there are about 170 plates. In the small specimen RM Ec 4432 their number was estimated at 120 (for size of the specimen, see above). The basal circlet is formed by 7 plates in the larger specimen, but no system in the construction of the theca could be detected. The individual plates vary a good deal in shape. Extraordinarily large plates measure about 6 mm. The sutures are often visible in contrary to the case of the preceding species.

**Pores of the thecal plates.** The plates have a considerable number of diplopores. In a large plate they were estimated at 60. The pores are enclosed by peripores, the confluent walls of which form a low network all over the plates. The peripores are polygonal (not rounded as is often the case in the preceding species, where the walls of the peripores are thicker and higher). In the present species the test is smooth upon the whole, since no knobs or spines are developed in the walls of the peripores. The pores are distributed all over the plates without leaving a narrow marginal zone devoid of pores.

**The ambulacral system** is remarkably better preserved than in *Sphaeronites pomum* (see Pl. 12, figs. 3, 5. Pl. 13, fig. 1. Text-fig. 19:5). As in the preceding species, the ambulacral elements are concentrated in the neighbourhood of the mouth and in intimate connexion with the anus. Three ambulacra radiate from the centre, viz. one in radius III and one at each side. The grooves last mentioned divide at a short distance from the centre, the left one branching into each of the radii I and II, the right one in equal way into each of the radii IV and V. In good specimens it is clearly recognizable that the number of brachiole-facets at the end-point of each ambulacrum is subject to variation. Thus there may be one, two, or three of them (cf. the figs. referred to).

**Alimentary canal.** The mouth is not directly visible, being covered by 5 interrarial plates, which may be termed *OO*. The subcircular or oval anus is covered by a flat pyramid. Details of the anal pyramid could be made out in a few instances only, and it is remarkable that in all of them the number of valvules was stated at 6 or 7.

At the upper left side of the periproct there is a small pore opening in a protuberance, which is connected with the ambulacral area by a short, curved canal leading to the neighbourhood of the endpoint of the ambulacrum in radius I. A pyramid of 3 valvules covering the pore — as represented in ANGELIN's Pl. 11, fig. 9 — was not ascertained in the holotype, nor in any other specimen. It can hardly be doubted that this pore is the gonopore, in accordance with the interpretation given already by LOVÉN (1867, p. 439; 1868, p. 181) and by ANGELIN (1878 a, in the explanation of figs.). In a reproduction of ANGELIN's figure just quoted, BATHER (1900, p. 72) designated this aperture as madreporite. In a subsequent paper (BATHER 1919, p. 322) he announced a different opinion, taking the opening in question as the gonopore. LOVÉN, in the papers referred to above, suggested that the canal or, as was supposed, ridge running to radius I would indicate a madreporite. A more plausible explanation is that given alternatively by BATHER (1900, p. 72, fig. 39) in reproducing LOVÉN's figure (for reasons given p. 168, foot-note 10, above, this fig. undoubtedly represents *Sphaeronites globulus* and not *Sphaeronites pomum* as previously suggested). Here he proposed that the pore might represent a combined hydropore and gonopore.

The basal portion of the theca in several cases is seen to taper, thus acquiring the character of a broad, stem-like prolongation. In this species the structure of the base-surface gives no information on the substratum preferred by these organisms.

**Remarks:** — The differences between this species and *Sphaeronites pomum* might have appeared so clearly from the descriptions of the two forms that a repetition would be superfluous. The Norwegian form determined by BRÖGGER (1882, p. 42, foot-note 1) as a variety of *Sphaeronites globulus* has not been described and therefore cannot be taken into consideration. *Sphaeronites shittienensis* (REED 1917), from Ordovician strata of Yunnan with a supposed equivalence to the Platyrus limestone in Sweden, has a greater similarity to *Sphaeronites globulus* than to *Sphaeronites pomum* but displays no very close relation to the first-mentioned species either. Especially the location of mouth and anus is a different one in the East Asiatic species, where the two openings lie considerably apart. The other species of "*Sphaeronis*" from the same area described by REED (1917, p. 12), *Sphaeronis lobiferus*, evidently does not belong to *Sphaeronites* but rather to *Haplosphaeronis*.

**Regional distribution:** — Sweden, Öland: Böda Harbour (numerous specimens). — Östergötland (closer locality not known; 3 specimens). — Västergötland: Kinnekulle (1 specimen). — Dalarna: Fjäckå, Furudal, Gulleråsen (7 specimens). — ? Norway.

**Stratigraphic range:** — Lower Chasmops limestone (Upper Ilandeilian).

It should be mentioned, finally, that in the material available to the writer there are some poorly preserved specimens from the Gigas limestone in Öland probably referable to *Sphaeronites*. Some other likewise presumptive representatives of *Sphaeronites* originate from Kullsberg, Dalarna.

### Genus *Haplosphaeronis* JAEKEL 1926.

**Genotype:** — *Haplosphaeronis kiaeri* JAEKEL 1926.

**Synonyms:** — *Sphaeronis* (ex parte) auctorum. — *Sphaeronites* auctorum. — *Pomocystis* HAECKEL 1896. — *Pomosphaera* HAECKEL 1896.

**Diagnosis:** — A genus of Sphaeronitidae with ovoid or spheroidal theca attached directly with the basal surface; theca composed of two circlets, the lower one of 7, the upper one of 5 plates; numerous diplopores all over the surface of the plates, partly radially arranged; pores within elongated, often dumb-bell-shaped peripores with raised margins; the individual ambulacra branching fan-like; anus close to the mouth; gonopore at the upper left side of the anus.

**Regional distribution:** — Sweden, Norway. ? Yunnan (cf. p. 170 above).

**Stratigraphic range:** — Upper part of Middle Ordovician (and lower part of Upper Ordovician).

### *Haplosphaeronis oblonga* (ANGELIN 1878).

Pl. 10, figs. 5—10. Pl. 11, figs. 1—5. Text-fig. 22: 1.

1878 *Sphaeronis oblonga* ANG. — ANGELIN 1878 a, p. 30, Pl. 11, figs. 17—18.

1878 *Sphaeronis minuta* ANG. — ANGELIN 1878 a, p. 31, Pl. 11, figs. 21—22.

1878 *Sphaeronis uva* ANG. — ANGELIN 1878 a, p. 31, Pl. 11, figs. 23—24.

1878 *Sphaeronis sulcifera* ANG. — ANGELIN 1878 a, p. 31, Pl. 11, figs. 19—20.

1883 *Sphaeronis minuta* ANG. — TÖRNQUIST 1883, p. 20.

1888 *Sphaeronis minuta* A. — LINDSTRÖM 1888 a, p. 16.

1888 *Sphaeronis oblonga* A. — LINDSTRÖM 1888 a, p. 23.

1888 *Sphaeronis sulcifera* A. — LINDSTRÖM 1888 a, p. 23.

1888 *Sphaeronis uva* A. — LINDSTRÖM 1888 a, p. 23.

1890 *Sphaeronis oblonga* ANG. — HOLM, p. 269 (15).

1896 *Pomocystis uva* ANGELIN. — HAECKEL, p. 99.

- 1896 *Pomocystis sulcifera* ANGELIN. — HAECKEL, p. 99.  
 1896 *Pomocystis minuta* ANGELIN. — HAECKEL, p. 99.  
 1896 *Pomosphaera oblonga*, E. HAECKEL [sic!]. — HAECKEL, p. 99, fig. 9 (cop. from ANGELIN 1878 a).  
 1899 *Sphaeronites oblonga* ANGELIN. — JAEKEL, p. 398.  
 1919 *Sphaeronis oblonga* ANG. — FUNKQUIST, pp. 27, 19, Pl. 2, figs. 23, 23 a.  
 1927 *Haplosphaeronis Kiaeri* JAEKEL. — KLÆR, p. 8, fig. 2.

**H o l o t y p e:** — RM Ec 96.

**T y p e l o c a l i t y:** — Östbjörka, Dalarna.

**T y p e s t r a t u m:** — Kullsberg limestone, Middle Ordovician (and lower part of Upper Ordovician).

**M a t e r i a l:** — About 300 specimens.

**D i a g n o s i s:** — A species of *Haplosphaeronis*, the upper and lateral outlines of which are gently curved.

**D e s c r i p t i o n:** — The general shape of the theca is ovoid, spheroidal, or subquadrangular, with flat base and gently curved sides. A certain variation in shape is evident, as appears to some degree from the figs. on Pl. 10.

| (Measurements in mm)          | RM Ec<br>119 | RM Ec 96<br>(holotype) | UM ec<br>69 | Spec. in<br>SGU | RM Ec<br>103 | RM Ec<br>113 |
|-------------------------------|--------------|------------------------|-------------|-----------------|--------------|--------------|
| Height of the theca . . . . . | 24           | 22                     | 20          | 16.3            | 11.2         | 10.5         |
| Greatest diameter . . . . .   | 20           | 19.6                   | 20          | 14              | 13           | 11.5         |

The specimens in this table are those in Pl. 10, figs. 5—10.

**T h e c a l s k e l e t o n.** The construction of the thecal skeleton was mentioned in the diagnosis. The 7 plates of the basal circlet may be termed *LL*, in agreement with JAEKEL (1926, p. 19). They are rectangular or trapezoidal; in some specimens they are more elongated than in others (cf. Pl. 10, figs. 7 b and 8). The 5 plates of the second circlet have to be designated as *RR*. Those at each side of the anal interradius (*R* 5 and *R* 1) are irregularly hexagonal in outline, the others are pentagonal. According to JAEKEL (l.c.), two additional anal plates are intercalated in the interradius *V*—*I*, between mouth and anus. The presence of such plates was not ascertained by the author. On the contrary it could be stated safely that the area between mouth and anus is formed by the intimately amalgamated adoral parts of *R* 5 and *R* 1. There is namely no trace of sutures. Thus the specimen figured in text-fig. 22: 2 is not correctly represented as far as concerns the suboral area. The three larger plates and the small group of minute plates are not recognizable in the actual specimen. The thecal walls are rather strong, attaining a thickness of more than 1 mm (Pl. 11, fig. 2).

**P o r e s o f t h e t h e c a l p l a t e s.** The two openings of a diplopore are fairly wide apart. The system is enclosed by an elongated peripore with



slightly raised margins, often having the shape of a dumb-bell. In the specimen figured in Pl. 10, fig. 7, there are more than 100 pores in each of the *RR*. In the middle of the plates the long axis of the peripores is parallel with the long axis of the plate. Towards the periphery, the pores are arranged more or less radially.

The ambulacral area is subpentagonal (Pl. 11, fig. 1. Text-fig. 22: 1). The main grooves branch in the same way as described above for *Sphaeronites globulus*. The individual grooves, in their turn, branch fan-like, running to the facets of 3—4 brachioles. Each group of brachiole-facets rests on the adoral portion of the *RR*. A slit in *O 1* represents possibly the hydropore, as proposed by JAEKEL.

Alimentary canal. The mouth is not directly visible, being covered with 5 *OO*, of which *O 1* is broader than the others. The anus (diameter 3 mm in the specimen in Pl. 11, fig. 1) lies close to the peristome. It is covered by a flat pyramid, usually formed by 6 or 7 irregular valvules. A number of specimens have been sectioned, but in all cases examined the theca proved to be filled with matrix displaying no features of internal course of the alimentary canal.

The gonopore is a circular aperture between the anus and the ambulacral fan of radius I.

The base-surface is generally broad and flat. This may indicate that the animal has rested directly on the sea-floor. But in several cases it has been attached to other organisms, as demonstrated by specimens still connected with a coral- or bryozoan-stock or the theca of another cystoid (Pl. 11, figs. 4—5. Text-fig. 19: 6).

Discussion: — As appears from the list of synonyms above, several forms regarded by ANGELIN (and, following him, by subsequent authors) as distinct species have been thought not to be specifically distinguishable from *Haplosphaeronis oblonga*. The identification was proposed by JAEKEL (1899, p. 398), and the present writer cannot but agree. The several forms indicated by ANGELIN through specific names show namely no real difference from the holotype, irrespective of their minor size, or — as in "*Sphaeronis sulcifera*" — some fortuitous feature. The longitudinal stereom folds in the form mentioned (one unique specimen) no doubt are merely accidental. The small "*Sphaeronis minuta*" and "*Sphaeronis uva*" have to be looked upon as juvenile forms.

Unfortunately no specimens of the Norwegian *Haplosphaeronis kiaeri* JAEKEL 1926 were available to the writer. Judging from Pl. 1, fig. 2, in JAEKEL 1926 it differs from the Swedish species in the shape of the theca, which is mitre-like in outline when seen in lateral view. Thus the side-walls

form a clear angle with the upper walls. Yet this feature is not prominent in the fig. communicated by KLÆR (1927, p. 9). Further it was said to have 4 brachiole-facets on each *R*. This is of no diagnostic importance, however, for in the Swedish species they vary in number between 3 and 4. With regard to the shape of the plates in the lower circlet *Haplosphaeronis kiaeri* comes next to the Swedish forms with elongated *LL*. On the whole, the two forms seem to be most nearly related (maybe identical?). *Haplosphaeronis kiaeri* is very common in the so-called "Sphaeronid-shale" in Hadeland. The superimposed limestone contains a somewhat larger form designated by JAEKEL (1926, p. 21) as *Haplosphaeronis kiaeri* var. *norvegica*, differing to some extent in the number and position of the pores. The Norwegian *Haplosphaeronis*-horizon forms the top of the Ordovician sequence.

As mentioned above, "*Sphaeronis*" *lobiferus* REED 1917, from considerably older (Lower Llandeilian) strata in Yunnan, might be referable to *Haplosphaeronis*. Yet REED's description hardly admits of a safe conclusion.

**Regional distribution:** — Sweden, Dalarna: Amtjärn (numerous specimens), Arvet, Boda, Fjäckå, Hosjön, Kallholn, Lissberg, Skattungbyn, Skålberget, Vikarbyn, Östbjörka. — Västergötland: Kinnekulle. — Skåne: Tommarp.

**Stratigraphic range:** — According to THORSLUND (1935, p. 27; 1936, p. 26), *Haplosphaeronis* is characteristic of the Kullberg limestone. Yet it occurs also in the lower (Ordovician) part of the Boda limestone, as confirmed by specimens from Skålberget collected by THORSLUND and fixed stratigraphically by him. Indeed the main part of the localities verified by museum specimens are exposures of Boda limestone, though the material from Kullberg limestone is superior in numbers.

The unique Scanian specimen was derived from the so-called cystoid-shale, presumably representing Lower Chasmops beds. The single specimen from Västergötland may originate from an equivalent horizon.

Thus the species has a rather wide stratigraphic range, from Upper Llandeilian to some horizon of the Ashgillian not closely known.

Finally we have to report some finds of *Haplosphaeronis*, where a safe specific determination cannot be performed owing to the poor state of preservation of the specimens. Thus a fragment [SGU] was discovered at the 316.9 m level in the core from the deep-boring at File Haidar, Gotland (THORSLUND 1938, p. 28). Also in Jämtland representatives of the genus have been met with, namely at Tandsbyn (THORSLUND 1940, p. 55) and at Örån (THORSLUND 1940, p. 91). The specimens now mentioned are from strata of Chasmops age.

Genus *Eucystis* ANGELIN 1878.

**Genotype:** — *Eucystis raripunctata* ANGELIN 1878.

**Synonyms:** — See JAEKEL 1899 (p. 405). Addenda: *Carpocystites* OEHLERT 1887. — *Carpocystis* BATHER 1900.

**Diagnosis:** — A genus of Sphaeronitidae with rounded or elongated theca; theca composed of a moderate number of plates; 5 or 4 branching ambulacra, the longest grooves of which may extend into the circlet below the adoral one; anus apart from the mouth; theca attached directly with a flat basal surface, or provided with a short stem.

**Remarks:** — In agreement with JAEKEL (1899, p. 405), the present writer cannot see any reason why *Proteocystites* (syn. *Carpocystites*) should be regarded as a separate genus. It has namely all essentials in common with typical representatives of *Eucystis*. Whether the imperfect remains from the Ordovician of Yunnan described as *Eucystis* by REED (1917, p. 11) really belong there cannot be decided safely.

**Regional distribution:** — ? Yunnan (Middle Ordovician)—? Great Britain (Middle and Upper Ordovician; JAEKEL 1899, p. 406), Sweden [Upper Ordovician and (or) Lower Silurian], Germany (Lower Devonian; JAEKEL 1899, p. 407), Bohemia (Lower Devonian; JAEKEL l.c.), France (Lower Devonian; BATHER 1900, p. 73).

**Stratigraphic range:** — Middle (?) Ordovician—Lower Devonian.

*Eucystis raripunctata* ANGELIN 1878.

Pl. 13, figs. 3, 5, 7. Pl. 14, figs. 1, 3—7. Text-fig. 22: 4.

1878 *Eucystis raripunctata* ANG. — ANGELIN 1878 a, p. 31, Pl. 11, figs. 25—28.

1888 *Eucystis raripunctata* A. — LINDSTRÖM 1888 a, p. 23.

[Non *Eucystis* cf. *raripunctata* REED 1917, p. 11, Pl. 3, figs. 3, 3 a].

**Holotype:** — RM Ec 2370, an incomplete and considerably worn specimen.

**Type locality:** — ? Osmundsberg, Dalarna (in the old label accompanying the specimen the locality is given as "Östbjörka?").

**Type stratum:** — Boda limestone.

**Material:** — A rather extensive material of *Eucystis* was available to the writer. Since in many cases the state of preservation does not admit of making out the construction of the skeleton, one often has to refrain from a specific determination. Some 150 specimens were thought to belong to *Eucystis raripunctata*.

**Diagnosis:** — A species of *Eucystis*, the theca of which is composed of short (in part roughly square) plates, disposed in 4—5 irregular circlets;

total number of plates about 30 (the diagram communicated by ANGELIN 1878 a, Pl. 11, fig. 28 gives no true idea of the conditions in the holotype, several plates having been omitted); 5 branching ambulacra, sometimes reaching below the plates of the adoral circlet; pores sparse in the latero-posterior portions of the theca but rather abundant in the latero-anterior ones; basal portion of the theca usually prolonged, or with a short stem.

**Description of the holotype:** — The general shape of the theca cannot be stated exactly, for the basal portion is wanting. The rest of the theca is rounded in outline, and somewhat compressed from the sides, so that it is ovoid in transverse section. It is a little hump-backed.

**Measurements** (N. B. that the specimen is imperfect). Height 18 mm; greatest diameter 16 mm; diameter perpendicularly to that mentioned, 14 mm.

**Thecal skeleton.** Some of the plates are roughly quadrangular, but most of them are polygonal; they are not extended in longitudinal direction. The adoral circlet contains 6 plates. The remaining plates are not arranged in clearly defined circlets, but the following conditional survey of the contents of plates in the circlets (the adoral circlet is mentioned first) should give an idea of their disposition: — 6, 8+2 “anal plates”, 9, 5 (cf. also text-fig. 22: 4 b).

**Surface structures of stereom.** In some plates a fine granulation is visible, as illustrated by ANGELIN (1878 a, Pl. 11, fig. 27).

**Pores of the thecal plates.** As mentioned in the diagnosis, pores are sparse in the latero-posterior portions of the theca but more numerous in the latero-anterior parts. Thus nearly 50 pores were counted in a plate (7×7 mm) of the circlet below the adoral one and lying approximately in the interradius II—III. The pores are small, oval. The surface of the test being considerably worn — as is the case, moreover, in a good deal of the specimens — peripores are but traceable.

**Ambulacral system.** 5 ambulacra radiate from the mouth, one from each angle. Each ambulacrum gives off to the left 2 or 3 short side-branches ending in brachiole facets raised over the surface of the theca. All ambulacra, excepting that in radius II reach somewhat below the plates of the adoral circlet. The hydropore is visible as a transverse slit between the mouth and the anus, being bisected by the suture between two adorals.

**Alimentary canal.** The mouth is somewhat eccentric, lying to the right of the morphological apex of the theca. It is pentagonal and relatively small, with a diameter of 2.5 mm. The subcircular anus, in inter-radius V—I, is considerably larger (diameter 4 mm). It opens in the upper wall of the theca. No covering plates of mouth and anus are preserved.



The gonopore is a small opening at the upper left side of the mouth, between this and the proximal brachiole-facets of the ambulacrum in radius I.

The basal portion, as mentioned, is not preserved.

Remarks on typoids: — From the figs. of *Eucystis raripunctata* in Pls. 13—14 it appears that the general shape of the theca varies a good deal. A stem or a stem-like prolongation seems generally to have been developed. The longitudinal thin-section in Pl. 13, fig. 5, shows the proximal portion of a true stem. In some specimens columnals are to be recognized. On the other hand there are specimens entirely devoid of a stem like that in Pl. 14, fig. 4, which is attached to a stem-fragment of a pelmatozoan directly with the basal surface.

The granulated surface of the plates is well visible in Pl. 13, fig. 7. Here the peripores also are unusually well preserved, on account of which the pores seem to be exceptionally crowded.

In most cases the ambulacra are not as long as in the holotype. Where more concentrated, the elevations supporting the brachiole-facets of each ambulacrum flow together so as to form irregular swellings.

Discussion: — No foreign species known to the writer shows any close affinity to *Eucystis raripunctata*. The main characters distinguishing it from other congeneric Swedish forms will be indicated shortly.

*Eucystis acuminata* n. sp. differs i.a. by its prolonged adoral plates calling forth a tapering of the theca towards the oral pole; the anus opens in the side-wall and not in the upper wall.

In *Eucystis angelini* n. sp. the thecal skeleton is composed of an inferior number of plates which, further, are more regularly arranged.

*Eucystis quadrangularis* n. sp., finally, differs from all other conspecific forms in the reduction of the ambulacrum in radius III.

Regional distribution: — Sweden, Dalarna: Arvet, Boda, Lissberg, Osmundsberg, Skålberget, Östbjörka.

Stratigraphic range: — THORSLUND (1935, p. 27; 1936, p. 26) pointed out that *Eucystis* is characteristic of strata contained in the Boda lime-stone. Probably it occurs especially in marly beds. Whether *Eucystis raripunctata* ranges through the whole of the Boda limestone (the Upper Ordovician as well as the Lower Silurian part) is not known to the writer.

***Eucystis angelini* (LOVÉN MS) n. sp.**

Pl. 13, figs. 4, 6. Text-fig. 22: 3.

1936 *Eucystis* sp. — THORSLUND, Pl. 2, figs. 17—18.

Derivation of name: — The species is named in honour of N. P. ANGELIN (1805—1876).

**Holotype:** — RM Ec 2375.

**Type locality:** — Boda, Dalarna.

**Type stratum:** — Boda limestone, Upper Ordovician or Lower Silurian.

**Material:** — About 70 specimens.

**Diagnosis:** — A species of *Eucystis*, the theca of which is composed of 22 plates in 3 circlets of (from below) 7, 8, 5 plates, and 2 additional "anal" plates; most plates of the two lower circlets elongated; 5 short branching ambulacra, which do not reach below the plates of the adoral circlet; thecal pores small, not very abundant, not, or occasionally, developed in the plates of the basal circlet; theca attached with a broad surface.

**Description of the holotype:** — The general shape of the theca is ovoid, tapering in basal direction and with flattened upper surface. It is subpentagonal in transverse section. The left half of the theca is somewhat inflated.

**Measurements of the theca.** Height 17 mm; greatest diameter (in the transverse plane) 12 mm; diameter perpendicularly to that mentioned, 11 mm.

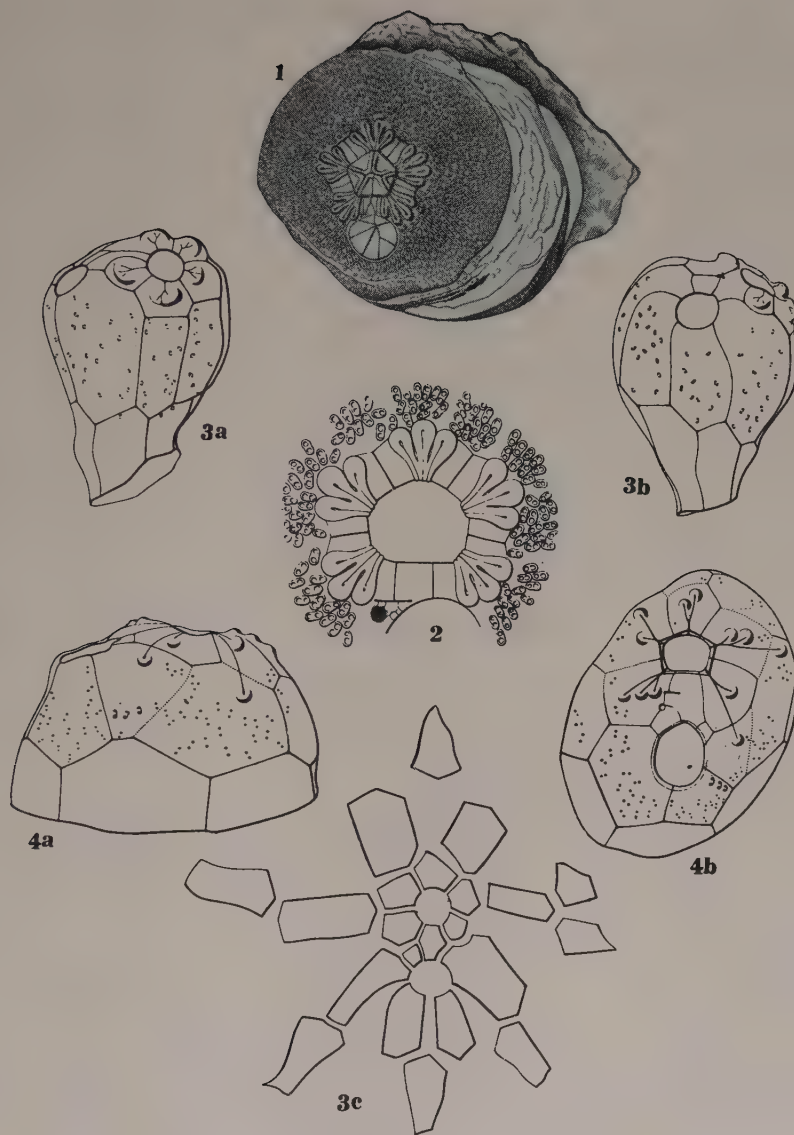
**Thecal skeleton.** The 22 plates constituting the theca are arranged in 3 circlets, as follows: — The basal circlet contains 7 unequally-shaped plates, in part narrow and elongated. The middle circlet consists of 8 narrow and elongated plates, and the adoral one of 5 smaller plates; in the anal interradius 2 additional plates are intercalated, one between the mouth and the anus, and one between the adoral plate in the radius I and the anus (cf. text-fig. 22: 3 c).

**Pores of the thecal plates.** The small, oval diplopores are confined to the two upper circlets, especially to the middle one. Thus one of the largest plates (that in the interradius I—II) contains only some 20 pores.

**Ambulacral system.** The 5 ambulacra are very short and do not reach below the plates of the adoral circlet. They are situated on knob-like elevations. Their mode of branching is not clearly visible in the holotype. Each ambulacrum is connected with 2 or 3 brachiole-facets. The slit-like hydropore is bisected by the suture between the adoral plate in radius I and the "anal" plate to the right of it.

**Alimentary canal.** The mouth is circular, with a diameter of 2.5 mm. It is eccentric, lying obliquely to the right of (and in front of) the anus. This is circular, too, and has a diameter of 3 mm. It is separated from the mouth by the length of the intercalated "anal" plate.

The gonopore lies at the foot of the ambulacral elevation in radius I, where the sutures between the adoral plate in radius I and the two "anal" plates meet.



Text-fig. 22. 1. *Haplosphaeronis oblonga* (ANGELIN) [RM Ec 116], upper face; about  $\times 3$ . Fjäckå, Dalarna. 2. The same species, circumoral area. 3. *Eucystis angelini* (LOVÉN MS) n. sp., holotype [RM Ec 2375], 3a right lateral view; 3b right latero-posterior view; about  $\times 2$ ; 3c analysis of the theca. Boda, Dalarna. 4. *Eucystis raripunctata* ANGELIN [RM Ec 2376], 4a right lateral view; 4b upper face, about  $\times 3$ . Arvet, Dalarna. (From LOVÉN MS, Pl. 10; numbering by the present writer. About  $\frac{2}{3}$  of original size.)

The obliquely concave base-surface indicates that the specimen was attached to some coral or bryozoan stock.

Remarks on typoids: — Some additional features may be derived from the fine specimen figured by THORSLUND (1936) [SGU], here represented in Pl. 13, fig. 4. The plates of the basal circlet are somewhat shorter and broader. In some specimens the feature last mentioned is still more pronounced, so that the theca is almost cylindrical. Certain specimens, on the other hand, are more pyriform. The ambulacral area is better preserved in the specimen referred to. All ambulacra, maybe excepting that in radius III, show 3 short branches and thus have 3 brachiole-facets.

The plan of construction of the theca with a definite number of plates, elongated in part, is sufficient to distinguish this specimen.

Regional distribution: — Sweden, Dalarna: Boda, Lissberg, Osmundsberg.

Stratigraphic range: — Boda limestone, Upper Ordovician and (or) Lower Silurian.

*Eucystis acuminata* n. sp.

Pl. 14, fig. 9.

Derivation of name: — From Lat. *acuminata*, tapering, alluding to the shape of the oral pole of the theca.

Holotype: — RM Ec 2173.

Type locality: — Gulleråsen, Dalarna.

Type stratum: — Boda limestone, Upper Ordovician or Lower Silurian.

Material: — Beside the holotype, two specimens [SGU] were available.

Diagnosis: — A species of *Eucystis*, the theca of which is composed of 31 plates (most of them roughly quadrangular or rectangular) disposed in 5 regular circlets of (from below) 4, 7, 7, 7, 5 plates, and one additional "anal" plate; 5 short branching ambulacra, which do not reach below the plates of the adoral circlet; thecal pores small, fairly numerous; no stem.

Description of the holotype: — The general shape of the theca is subelliptical. The theca is compressed in sagittal direction, being subelliptical in transverse section too.

Measurements of the theca. Height 38 mm; greatest diameter 23.3 mm; diameter perpendicularly to that mentioned, 18.7 mm.

Thecal skeleton. The elements of the skeleton are remarkably regular in shape as well as in arrangement. Thus the plates of the three



median circlets are roughly quadrangular or rectangular. In the adoral circlet they are wedge-shaped and somewhat elongated. The basal circlet contains 4 plates, each of the three median circlets 7 plates, and the adoral circlet 5 plates. An additional "anal" plate is intercalated in the adoral circlet, between the mouth and the anus.

**Pores of the thecal plates.** Small ovate diplopores surrounded by peripores with raised margins are distributed all over the theca. In the plate in interradius I—II in the circlet below the adoral one about 60 diplopores were counted.

**Ambulacral system.** The 5 short ambulacra are situated on low stereomic elevations. They seem to have 2 or 3 branches corresponding to an equal number of brachiole-facets. — The slit-like hydropore lies partially on the ambulacral elevation in radius I. It is bisected by the suture between the adoral plate in radius I and the "anal" plate (Pl. 14, fig. 9 b).

**Alimentary canal.** The mouth is oval, with a long diameter of 4.5 mm. The anus (diameter 6 mm) opens in the side-wall of the theca.

The circular gonopore lies 1 mm below the hydropore and is bisected by the same suture.

No stem has been present but the theca was attached directly with the relatively narrow base-surface.

**Remarks.** The two other specimens agree well with the holotype. One of them is smaller (height 21 mm) and is less strongly compressed.

The species is well characterized by the tapering oral pole and by the construction described of the thecal skeleton.

**Regional distribution:** — Sweden, Dalarna: Gulleråsen (Lissberg).

**Stratigraphic range:** — Boda limestone, Upper Ordovician and (or) Lower Silurian.

### *Eucystis quadrangularis* n. sp.

Pl. 14, figs. 10—12, 14.

**Derivation of name:** — The name alludes to the shape of the mouth.

**Holotype:** — UM ec 2.

**Type locality:** — Kallholn, Dalarna.

**Type stratum:** — Reddish grey, splintery Boda limestone, Upper Ordovician or Lower Silurian.

**Material:** — About 35 specimens were available [RM, SGU, UM].

**Diagnosis:** — A species of *Eucystis* with pyriform theca; 4 well-developed branching ambulacra; thecal pores small, distributed all over the theca, relatively abundant; a well-developed stem is present.

**Description of the holotype:** — General shape of the theca. The theca is pyriform, tapering in basal direction to get produced into a stem.

**Measurements.** Height of the theca 22 mm; greatest diameter 20 mm.

**Thecal skeleton.** In the holotype, as in most other specimens, the sutures are so obscure that an analysis of the theca cannot be performed.

**Pores of the thecal plates.** Small rounded or oval diplopores are distributed rather uniformly all over the theca.

**The ambulacral system** is characterized by the suppression of the ambulacrum in radius III. The four remaining ambulacra are well developed. They are not as long as in *Eucystis raripunctata* but surpass the other species in this respect. The ambulacrum in radius V is lacking along with part of the test. The other ambulacra all have 4 branches running to large, kidney-shaped brachiole-facets. The ambulacra rest on small elevations. The hydropore can be traced as a transverse slit close to the proximal brachiole-facet in the ambulacrum of radius I. It is bisected by the suture between two adorals.

**Alimentary canal.** The mouth is rectangular, with a length of 4 mm. The anus is large, circular, measuring 5.5 mm in diameter; the same length has the space separating the anus from the mouth.

The gonopore is a small round opening beneath the hydropore.

The stem is broken at its base in the holotype. The diameter of the fracture is 5 mm.

**Remarks on typoids.** By combining observations on two specimens [RM Ec 1877, UM ec 1] the construction of the thecal skeleton could be made out rather safely. The plates are arranged in four regular circlets containing (from below) the following number of plates: — 4, 9, 9, 5, and 1 additional "anal" plate between the anus and the adoral of radius I. The individual plates are mainly pentagonal or hexagonal.

A well-developed stem is shown in the specimens figured in Pl. 14, figs. 11—12.

By the character of the ambulacral system, this species differs from other known forms of *Eucystis*. Otherwise it has a superficial resemblance to *Eucystis flava* (BARRANDE), from the Lower Devonian of Bohemia. In the tetramerism of the ambulacral system it agrees with certain species of

*Holocystites* (cf. BATHER 1919, p. 255 seq.) but is easily distinguishable by its long, branching ambulacra.

**Regional distribution:** — Sweden, Dalarna: Kallholn, Lissberg, Osmundsberg, Skålberget.

**Stratigraphic range:** — Boda limestone, Upper Ordovician (confirmed by specimens collected by P. THORSLUND with a note on the geologic horizon by the collector) and (?) Lower Silurian.

It was mentioned above that certain forms of *Eucystis* do not admit of a safe specific determination. Such a form — *Eucystis* sp. — with very irregular plating and high ambulacral elevations is figured in Pl. 14, fig. 2. Another one, with encrusting basal surface, is shown in text-fig. 19: 10.

### Family **Aristocystitidae** (NEUMAYR) BASSLER 1938?

Genus *Holocystites* HALL 1864?

*Holocystites*? sp.

Pl. 15, figs. 2—4.

1878 *Megacystis alternata* HALL var. — ANGELIN 1878 a, p. 30, Pl. 19, figs. 19—20.

**Locality:** — Kinnekulle, Västergötland. In the labels accompanying the specimens figured by ANGELIN (our Pl. 15, figs. 2, 4), "Kinnekulle" is followed by a mark of interrogation. Since a third specimen available (Pl. 15, fig. 3) is provided with definite statements of locality and horizon, we may take the information given for granted.

**Stratum:** — Grey limestone in the Dalmanites series, basal Silurian.

**Material:** — RM Ec 2738—2741, 2783, 3077.

**Remarks:** — The specimens under discussion are too fragmentary to be determined safely, chiefly since nothing is preserved of the ambulacral area. BATHER (1919, p. 74) also remarked that ANGELIN's "*M. alternata* HALL, var." "may have belonged to any large elongate Sphaeronid of Ordovician age". Yet there is some ground for proposing tentatively that we have to do with representatives of *Holocystites* (syn. *Megacystis* ANGELIN). First, there is a clear resemblance in habit between this form and American species of *Holocystites* (cf. e.g. HALL 1867, Pl. 12, figs. 1—9; FOERSTE 1917, Pl. 11, fig. 4; FOERSTE, 1920 b, Pl. 4). Of greater importance is that a pore-structure, with irregular channels joining the diplopores in groups, characteristic of *Holocystites*, is traceable. But for reasons given it seems to be wisest not to propose an unreserved identification.

In this connexion a few words may be said of the form figured in Pl. 15, fig. 1 [spec. in SGU]. The theca is composed of rather large poly-

gonal plates. The structure of the pores recalls that of *Holocystites*. The oro-anal area, which is poorly preserved, rather suggests affinity to *Sphaeronites*, however. In lack of good specimens the form is left undetermined.

### Indeterminable forms:

1. "*Megacystis ovalis* ANG." (ANGELIN 1878 a, p. 30, Pl. 27, fig. 13). The type specimen (from Dalarna) has not been traced, nor any other specimens very similar to ANGELIN's figure. Cf. yet p. 137 above. It is clear that the form belongs to the Rhombifera.

2. "*Sphaeronis? dalecarlica* ANG." (ANGELIN 1878 a, p. 31, Pl. 27, fig. 9), Pl. 14, fig. 13. The specimen [RM Ec 2378], according to the label from "Dalarne. Osmundsberget? Boda?", is badly crushed. There are a great many polygonal plates with small, crowded diplopores. ANGELIN (l.c.) spoke of the species as "valde dubia, forsan *Glyptosphaera*". It is true that there is some resemblance to *Glyptosphaerites* in pore-structure, but no ambulacra extending over the theca are visible. In the author's opinion this specimen cannot be determined generically.

3. The form figured in Pl. 14, fig. 8 [spec. in LM]. The small theca (height 10 mm) seems to consist of plates disposed in 3 circlets, of about 6—7 plates in each. A large circular anus is visible, as well as scattered minute pores, the structure of which cannot be recognized. The actinal region is destroyed. Among known genera, *Eucystis* displays some resemblance but an identification would be too doubtful. The specimen originates from the Staurocephalus shale (uppermost Ordovician) by Tommarp, SE Scania.

4. "Cystoid", from red limestone in the Chasmops series at Älleberg, Västergötland, mentioned by WALLERIUS (1894, p. 300). The specimen alluded to was found in the LM collection by the present writer. It is a poor fragment that cannot be determined. The rock is yellowish rather than red.

5. "Cystoid", from the Dalmanites series (basal Silurian) in the Kinnekulle Mountain, mentioned by TROEDSSON (1921, p. 11). The specimen [in LM] was examined by the writer. Undeterminable.

Finally it may be recalled that TULLBERG (1882 c, p. 19) announced "cystoids" from the zone of *Calymene dilatata* (Chasmops series) in Scania. The same author (TULLBERG 1883, p. 5) listed a "cystoid" from the Orthoceratite limestone in Kvarnbäcken, Röstånga, Scania. His statement was repeated by MOBERG (1910, p. 120). According to MOBERG the horizon is Asaphus limestone. The present writer has not seen any of the specimens mentioned by TULLBERG.



Subclass **Blastoidea** SAY 1825.Order **Coronata** JAEKEL 1918.Family **Stephanoblastidae** JAEKEL 1918.Genus ***Paracystis*** SJÖBERG 1915, emend. auct.

Genotype: — *Paracystis ostrogothicus* SJÖBERG 1915.

**Diagnosis:** — A genus of Stephanoblastidae with adorally pentagonal and basally trigonal theca, the slightly arched lateral outlines of which (projected into the vertical plane) converge slightly and are bent strongly inwards only near the base; interrarial prolongations of *RR* blunt; *RR* flexed along their medial (radial) line at an angle of  $110^\circ$  (measured at the edge of the adoral surface); one rounded radial keel running straight down coalescing with one keel from each of the two neighbouring radial corners, so as to form the pointed (radial) termination of one *B*, the (interrarial) ends of the other two *BB* being formed by the fusion of each two neighbouring radial keels; ends of *BB* reaching below the point of attachment of the stem; ornamentation on skeleton plates of well-marked ridges arranged so as to form a system of 8 rhombs and 8 demi-rhombes (strictly speaking, some part of the other half of the demi-rhombes is also present; it need not be emphasized that the terms "rhombs" and "demi-rhombes" do not apply to pore-rhombes, as in the case of Hydrophoridae Rhombifera), all of these rhombes and demi-rhombes being bisected by the suture-lines; 3 demi-rhombes and the lower halves of the rhombes belonging to the *BB*, 5 demi-rhombes and the upper halves of the rhombes belonging to the *RR*; ambulacral grooves petaloid.

**Regional distribution:** — Sweden.

**Stratigraphic range:** — Middle Ordovician.

***Paracystis ostrogothicus*** SJÖBERG 1915.

Pl. 15, fig. 5. Text-figs. 23—24.

1915 *Paracystis ostrogothicus*. — SJÖBERG, p. 173, Pl. 2, figs. 1—2; Pl. 3, figs. 1—5.

**Holotype:** — The specimen figured by SJÖBERG 1915, Pls. 2—3. [LM].

**Type locality:** — The shore of lake Vättern SW of Radbandet (geol. map-sheet Motåla), Nässja, Östergötland.

**Type stratum:** — Limestone in the upper part of the Chasmops series, Middle Ordovician.

**Material:** — One single specimen, the holotype.

**Diagnosis:** — Coincident with that of the genus, one species only being known.

**Description:** — General shape of the theca. The theca has the shape of a frustum of a pyramid (inverted), pentagonal at the adoral surface and trigonal at the base in the way mentioned in the diagnosis of the genus, the sides with gently curved outlines. The five main keels beginning at the distal ends of the ambulacral grooves contribute decidedly to constitute the pentagonal shape of the transverse plane in the oral region. As said in the diagnosis, one keel runs straight down, coalescing with two adjacent keels, one from each side, whereas the remaining four keels meet two and two. Thus each of the three *BB* becomes provided with a strong keel.

**Measurements.** Height of the theca (interradial prolongations of radialia not included) 4.5 mm. Diameter of theca at the adoral surface 4.8 mm.

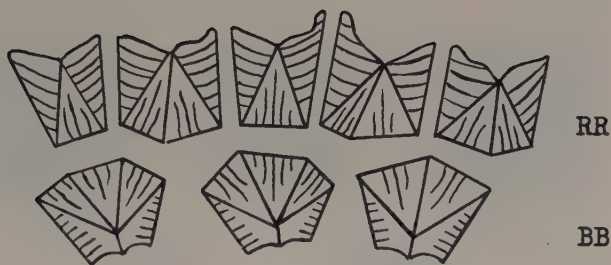
**Thecal skeleton.** As mentioned above (p. 32), the analysis of the thecal elements published by SJÖBERG (1915) is incorrect throughout, owing to the fact that certain well-marked ridges of the surface ornamentation were interpreted as sutures, whereas the true sutures, indeed very difficult to recognize, were almost completely overlooked. On that account *Paracystis* was conceived as a very aberrant pelmatozoan type. The analysis performed by the present writer with the aid of better optical equipment than that available to his predecessor and with a perfect source of illumination, which proved highly necessary, affords a quite different picture, placing *Paracystis* into the Blastoidea.

Unfortunately the orientation of the theca remains unsettled, since the position of the anal interradius could not be determined (cf. p. 187 below, foot-note 1). The thecal plates are arranged according to the ordinary scheme of Blastoidea, with 3 *BB* and 5 *RR*.

Two of the *BB* are heptagonal in outline and the third hexagonal. Each *B* consists of a larger, strongly keeled medial portion produced into a short, curved, rostrate termination, and two smaller lateral, subtriangular portions, sloping downwards. Thus the base of the theca shows three immersed subcordate fields, formed by the lateral portions of two adjacent plates, alternating with three keeled portions.

The five *RR* are developed as fork-pieces, though, on account of the imperfect state of preservation, most of the interradial prolongations of the *RR* are lacking in the actual specimen. The only preserved interradial prolongation has the shape of a short, blunt spine. The other four spines, which prove their presence only by triangular crystalline cleavages, may have had about the same shape. Two *RR* border on the *BB* by straight sutures and three of them by sutures inclined at a certain angle. The *RR* are flexed along the medial line, their lateral portions forming an angle of  $110^{\circ}$  at the edge of the adoral surface.

Text-fig. 23. *Paracystis ostrogothicus* SJÖBERG. Analysis of the theca in the holotype [LM].

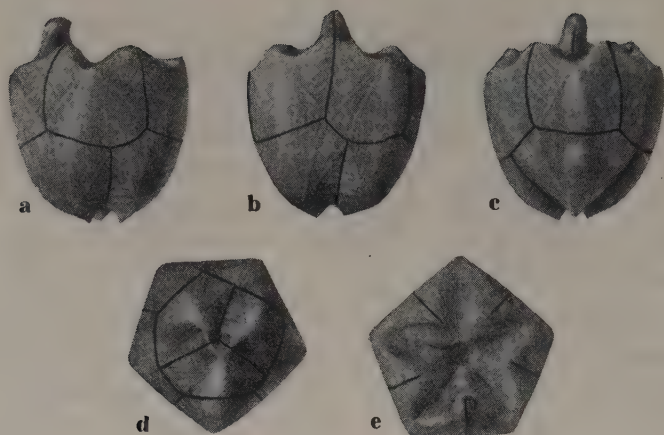


OO were not very likely to be preserved, and in fact, they could not be traced, not even in the case of the only interrarial prolongation present.

**Surface structures of stereom.** The main features of the thecal ornamentation were emphasized above in giving the diagnosis of the genus, and we have seen that the well defined ridges were mistaken for sutures in the original description of the species. These ridges, or rugae, are arranged so as to form 8 rhombs and 8 demi-rhombs (cf. the observation to the term demi-rhomb in the diagnosis). The sutures bisect the rhombs along the short diagonal and the demi-rhombs along the part present of the long diagonal, the lower halves of the rhomb being located to the BB and the upper halves to the RR. The distribution of the different surface structures on the several plates appears from the diagram of the theca (text-fig. 23).<sup>1</sup> Of the eight rhomboidal figures, seven are more or less vaulted along their long diagonal and coincide with the keels spoken of above, which are of great importance for the general shape of the theca. One rhomb is almost flat. The five broader rhombs were referred to by SJÖBERG as "radialia" and the three narrow rhombs as "radialia supplementaria". The long diagonal of the rhombs forms a certain angle to the vertical axis of the theca, only in the case of one rhomb is it sub-parallel (in the radius opposite to the interradius with preserved interrarial spine). The rhombs are

<sup>1</sup> The ornamentation of the BB may possibly serve as a guide at an attempt to determine the orientation of the theca. The trimerous base of Blastoidea is generally considered a secondary acquisition, which must be, however, of very old date, for, as stated MOORE 1940, p. 579, the "blastoids were derived evidently from an echinoderm stock that was already specialized in having the basal circlet reduced to three plates, for this character is seen in the earliest blastoids as well as in the latest". Then it may possibly be presumed that the BB to the left and in the middle of the diagram, which are tolerably uniform and have both three demi-rhombs, represent the plates corresponding to each two plates of the primary pentamerous basal circlet, the B to the right in the diagram being unfused. It differs in shape from the two other BB and has two demi-rhombs only. According to BATHER 1900 (p. 145) the Stephanocrinidae have three BB, "the unfused B being usually r. ant. as in Blastoidea", i.e. this plate is in the right anterior interradius according to the symbols used by BATHER. In the symbols of JAEKEL this would mean interradius III—IV. The right B of the diagram being the unfused one, the RR would get the following designations, from the left to the right: — 2, 1, 5, 4, 3.





Text-fig. 24. *Paracystis ostrogothicus* SJÖBERG, holotype [LM]. a—c The theca in different lateral views. d Basal view. e Oral view.  $\times 5$ . — Östergötland: Nässja. (From SJÖBERG 1915, Pl. 3. Sutures delineated by the present author).

provided with faint, somewhat irregular ridges, running tolerably parallel to the long diagonal. The number of ridges varies between 3 and 10, depending on the width of the rhomb. As far as can be discerned, the six quarters of rhombs belonging to the *BB* have 7 well-defined transverse ridges each, and the ten quarters of rhombs belonging to the *RR* about 8 less prominent ridges each, the ridges of two adjacent plates forming a certain angle. — The surface of the only interrarial spine present shows, when examined under the binocular, a number of pointed impressions, giving rise to a reticulate structure. This spine was called “proboscis” by SJÖBERG, who added, however (p. 175), that it seems to be pierced by delicate pores at the distal end, because of which the organ should possibly be interpreted as ovarian opening rather than anus. But as far as the writer can decide, no pores are present but only impressions in the stereom.<sup>2</sup>

**Hydrosfire-apparatus.** Neither hydrosfire-slits nor spiracles could be detected on examination of the exterior of the specimen. Yet the question whether hydrosfires are developed or not, could not be positively answered, principally on account of the imperfect state of preservation of the actinal region but also on account of the small size of the theca. The holotype being the unique representative at hand of the genus, no thin-sections could be prepared for a definite statement.

**Ambulacral system.** The shape of the ambulacra, which are confined to the adoral surface, may be described as petaloid, the sides not being straight and parallel but apparently gently curved. As for the nature

<sup>2</sup> If the orientation of the theca is that for which a certain reason of probability was assigned in foot-note 1, p. 187, the process proposed by SJÖBERG to be a proboscis, would not be in the anal interradius V—I but in the interradius IV—V. It is true, however, that in many Cystoidea the anus does not lie in the interradius V—I, and in those cases it is always pressed back to interradius IV—V (JAEKEL 1918, p. 8).



of plates flooring, roofing, and edging the ambulacral grooves we are left again in uncertainty because of the poor state of preservation. So nothing can be said about the insertion of brachioles.

A h y d r o p o r e was not observed.

A l i m e n t a r y c a n a l. Of organs belonging to the alimentary system nothing but the mouth is visible, which lies as a rounded opening in the centre of the adoral surface. Eventual covering plates of the peristome are no more preserved than the rest of the skeleton elements of the actinal region. The position of the a n u s cannot be fixed. As mentioned above, the process interpreted by SJÖBERG as proboscis is nothing but one of the interrarial spines of the radialia. Instead, the anus was certainly located either to the ventral side of the (posterior) interrarial spine V—I, as in *Tormoblastus*, or to the base of the same spine, as in *Stephanocrinus*.

G o n o p o r e. The gonopore and the hydropore not being visible, we may conclude that, in *Paracystis*, they have migrated into one of the intestinal openings, presumably the anus, forming a cloaca in the same way as in certain Carpoidea (cf. GISLÉN 1930, p. 215).

S t e m. It cannot be stated safely if *Paracystis* was stalked or not. Between the BB there is a small rounded invagination which can, however, possibly be the point of attachment of the theca on a faint stem. An opening piercing the bottom of the theca could not be detected.

D i s c u s s i o n: — SJÖBERG (1915, p. 176) called attention to the rather considerable resemblance between *Paracystis* and *Stephanocrinus*, which was thought, however, to be merely superficial. For if we accept the analysis of *Paracystis* proposed by SJÖBERG the structure of the two genera must necessarily seem different enough. On account of the total lack of arms of the specimen, SJÖBERG was inclined to refer *Paracystis* to the cystoids, i.e. the Hydrophoridae. The Protoblastoidea of BATHER were also taken into consideration, but in that case too a closer connexion was thought improbable. Here it may be noted that BASSLER (1938, p. 13) placed *Paracystis* with a mark of interrogation in the Protoblastoidea, family Asteroblastidae, the members of which have all diplopores and should be referred to the Hydrophoridae Diploporita (cf. above p. 24). ZITTEL-BROILI 1924 (p. 177), also with a mark of interrogation, ranged *Paracystis* with the Stephanocrinidae, which were taken as a family of Crinoidea Fistulata. From the above description it might have appeared that *Paracystis* does undoubtedly belong to the Stephanoblastidae JAEKEL.

The genera referable to the group mentioned will be shortly reviewed below when discussing the generic position of *Tormoblastus*. On account of the imperfect state of preservation of the only specimen in hand, a detailed comparison between *Paracystis* and other known forms can hardly be done. The two Swedish blastoid genera detected as yet are well separated

from each other by the general shape of the theca, the surface structures of the skeleton, &c. The Middle Ordovician *Mespilocystites* BARRANDE (d 2 and d 4 of Bohemia) seems, in a certain way, to have some affinity to our Swedish form, viz. concerning the ornamentation. Specimens of *Mespilocystites* from Zahořany [RM Ec 5540--5541] are unfortunately too imperfect to permit an intimate study. As far as can be discerned from the figures of *Mespilocystites* given by BARRANDE 1887 (Pl. 38, figs. 9 A, 10 A), the thecal plates of this genus show a system of rhombs and demi-rhombs, much the same as in *Paracystis*. It is true that the sutures are hardly visible on BARRANDE's figures, but their relations to the rhombs and demi-rhombs of the surface ornamentation are very likely to recall the conditions in *Paracystis* as may appear more clearly from JAEKEL's fig. 102 (1918, p. 110). In other respects the resemblances are not very striking. Thus the adoral surface, which is in *Paracystis* pronouncedly pentagonal, seems to be in *Mespilocystites* more or less rounded. Further the shape of the interrarial processes is a different one and they are directed obliquely outwards, whereas in *Paracystis* they were obviously about perpendicular.

A surface ornamentation agreeing as a matter of principle with that described in *Paracystis* seems also to characterize the Silurian genera *Stephanocrinus* (cf. ETHERIDGE & CARPENTER 1886, Pl. 19, fig. 11) and *Stephanoblastus* (cf. JAEKEL 1918, fig. 103 F, p. 110; BARRANDE 1887, Pl. 31, case I, figs. 1—3: — "*Rhombifera?*" *mira*). The interrarial prolongations of the latter have about the same shape as those of *Paracystis* as far as they can be reconstructed. But the base is quite different in the two genera, tapering successively in *Stephanoblastus* but being in *Paracystis* smoothly rounded. Moreover, the base of *Paracystis* with the immersed point of attachment, is unique among known Coronata.

Regional distribution: — Sweden, Östergötland: near Nässja.

Stratigraphic range: — Upper Chasmops series, Caradocian.

### Genus *Tormoblastus* JAEKEL 1927.

Genotype: — *Tormoblastus bodae* JAEKEL 1927.

Diagnosis: — A genus of Stephanoblastidae with adorally pentagonal and basally rounded theca; interrarial prolongations of *RR* claw-like, about as long as the height of the theca below the adoral surface; strong, rounded ridges running from the distal end-points of the ambulacra towards the base of the *BB*, one ridge from each of the radii II and V, two ridges from each of the other radii, diverging basally so as to approach to the neighbouring ridge of the adjacent radius; at the base of the theca three semilunar swellings, each being located below one of the double ridges and

being bisected by the sutures of *BB*; surface of *RR* with elongated pits, being arranged obliquely in rows along the sutures; ambulacra with sub-parallel lateral outlines; anus opening at the ventral side of the interradial prolongation I—V, above its *O* and between its *RR*; stem rounded.

Regional distribution: — Sweden.

Stratigraphic range: Upper Ordovician or Lower Silurian.

*Tormoblastus bodae* JAEKEL 1927.

Pl. 15, fig. 6. Text-fig. 25.

1927 *Tormoblastus bodae*. — JAEKEL 1927 a, p. 4, Pl. 1, figs. A—E.

Holotype: — RM Ec 5805.

Type locality: — Boda (NW of the church), Dalarna.

Type stratum: — Red marl-shale embedded in the Boda limestone, Upper Ordovician or Lower Silurian.<sup>3</sup>

Material: — One single specimen, the holotype.

Diagnosis: — Coincident with that of the genus, only one species being known.

Description: — General shape of the theca. Theca small-sized, calycular, pentagonal at the edge of the adoral surface, rounded towards the base.

Measurements. Height of the theca, interradial prolongations of *RR* included, 4 mm. Diameter of theca at the adoral surface 3.5 mm.

Thecal skeleton. Two of the *BB* are pentagonal, about equal-sized, larger than the third one, which is nearly triangular and situated below the *RR* 3 and 4. Each of the three semilunar swellings present at the base of the theca is bisected by the sutures of the *BB*.

The five *RR* are, as usual in the Coronata, fork-plates, the interradial processes of which are very well developed, attaining about the same length as the theca below the adoral surface. They are slightly bent inwards, thus gaining a claw-like appearance.

The five *OO* are rather obscure but may be represented correctly in JAEKEL's figures. The *O* of the anal interradius differs in shape from those of the other interradia, as illustrated by JAEKEL (see our text-fig. 25).

Surface structures of stereom. The thecal skeleton of *Tormoblastus* is characterized by a very pronounced sculpture, the dominant

<sup>3</sup> According to kind information by Dr. P. THORSLUND (letter to the author), *Tormoblastus* probably originates from intercalations of red marl-shale in a rather high portion of the "Leptaena limestone", viz. from the quarry at the dip-symbols 65° and 35° NW of the church of Boda on the sketch-map communicated by THORSLUND 1936 (p. 43). Thus its age might be Lower Silurian rather than Upper Ordovician.



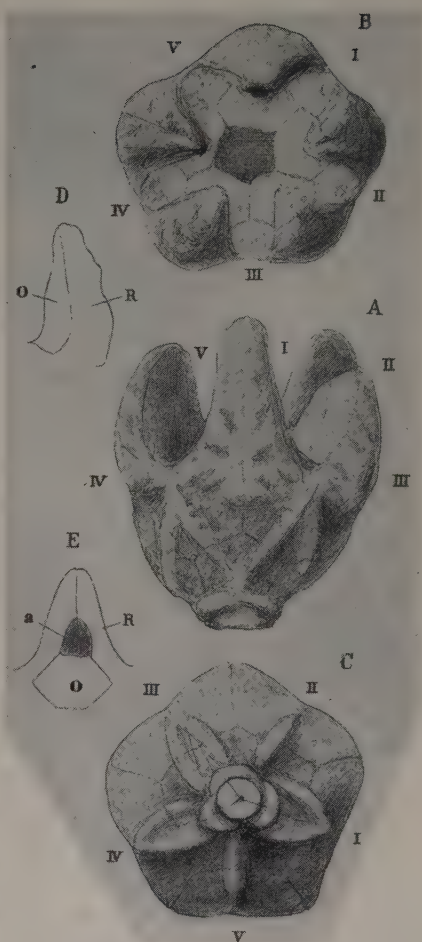
element of which consists of strong, rounded, fusiform ridges running from the distal ends of the ambulacra towards the base of the *BB*. As emphasized in the diagnosis of the genus, one ridge sets out from each of the *RR* 2 and 5, two ridges beginning at each of the other ambulacra. The double ridges diverge basally so as to approach to, or coalesce with, the base of the neighbouring ridge. The basal swellings are situated mainly between the two rays of the double ridges. The sides of the ridges are vaguely indented. The *RR* are impressed with shallow, elongated pits, which are arranged obliquely along the sutures.

**Hydrospire apparatus.** The eventual presence of hydrospires could not be ascertained, not the slightest trace of slits or spiracles being detected: either they are not developed or they are not visible in the actual specimen, which could not be sacrificed for preparing a slide.

**Ambulacral system.** The ambulacra do not reach below the adoral surface. They are elongated, with subparallel sides. Details of the pavement can unfortunately not be made out, nor can anything be said about the arrangement of the brachioles.

No hydropore is visible.

**Alimentary canal.** In the ordinary place, in the centre of the adoral surface and deeply immersed between the interradial prolongations, is the peristome with a rather big rounded opening, the mouth (in JAEKEL's drawing it is a little too angular). Covering plates or other skeleton elements of the peristome are not to be seen. The anus is a large triangular opening on the inside of the anal interradial process. It is situated above the *O* of this interradius and in the suture of the two adjacent *RR*. There are no traces of covering plates.



Text-fig. 25. *Tormoblastus bodae* JAEKEL, holotype [RM Ec. 5805]. A Lateral view. B Oral view. C Basal view. D A "normal" interradial prolongation in lateral view. E The anal interradius in internal face. I—V The five radii. O Oral. R Radius. a Anus.  $\times 5$ . — Dalarna: Boda. (From JAEKEL 1927 a, Pl. 1).



**Gonopore.** As was to be expected the gonopore is no more exposed than the hydropore. They are likely to have migrated into the anus.

**Stem.** *Tormoblastus* was provided with a rounded stem, as appears from the uppermost columnal, which is attached to the theca. The diameter of the stem is about a fifth of that of the theca. It is pierced by a narrow lumen.

**Discussion:** — *Tormoblastus* was referred to the Crinoidea (Inadunata-Larviformia) by BASSLER (1938, p. 185). We have endeavoured to show above (pp. 32—35) that *Stephanocrinus* and the small group of forms brought in connexion with it should conveniently be looked upon as blastoids, forming the paratypical order Coronata. The relation of *Tormoblastus* to the other genera of Coronata will be shortly reviewed.

*Mespilocystites* BARRANDE, with the single species *M. bohemicus* (BARRANDE), from the Middle and Upper Ordovician (the "bands" d 2 and d 4 of BARRANDE) of Bohemia, is the oldest known representative of the Coronata. Judging from BARRANDE's figures (1887, Pl. 38, figs. 3—5), *Mespilocystites* has a rather great resemblance to *Tormoblastus* with regard to the general shape of the theca but is well separated by several features. Thus it lacks the strong ridges passing from the *RR* to the *BB* in *Tormoblastus*. The ornamentation of the thecal plates is quite different in other respects, too. Also the shape of the prolongations is a different one, not being claw-like.

*Paracystis* SJÖBERG, described above, is also a Middle Ordovician genus and besides *Tormoblastus* the only Swedish blastoid known so far. Its affinities to *Tormoblastus* are no greater than in the case of *Mespilocystites*.

*Tormoblastus bodae* is as yet the only coronate blastoid from a horizon at the Ordovician-Silurian boundary, all species of the two more genera being confined to the Middle Silurian.

Several species of *Stephanocrinus* CONRAD have been reported from the Niagaran of North America (BASSLER 1915, p. 1187 seq.). The genus is represented in Britain also (BATHER 1900, p. 145). The surface structures of its skeleton plates are somewhat reminiscent of those of *Tormoblastus*. Clear differences are to be found in the construction of the ambulacra, which in *Stephanocrinus* are considerably more differentiated, and in the location of the anus, this aperture being situated in *Stephanocrinus* at the (ventral) base of the interradial process V—I, whereas in *Tormoblastus* it lies on the ventral side of the corresponding interradial process.

*Stephanoblastus*, finally, which was established in 1918 by JAEKEL to receive "*Rhombifera?*" *mira* BARRANDE (by BATHER 1900, p. 145, referred to *Stephanocrinus*) from the Upper Silurian (E 2, Ludlow) of Bohemia, has perpendicularly orientated interradial prolongations, short, triangular ambulacra, and no ridges crossing the thecal plates.

From all the genera here mentioned *Tormoblastus* differs by the basal swellings also, further by its minute size.

Regional distribution: — Sweden, Dalarna: Boda.

Stratigraphic range: — Upper Ordovician or Lower Silurian.

### Class **Carpidea** JAEKEL 1900.

#### Order **Soluta** JAEKEL 1900.

#### Family **Dendrocystitidae** (BATHER) BASSLER 1938.

#### Genus **Dendrocystites** BARRANDE 1887.

Genotype: — *Dendrocystites sedgwicki* BARRANDE 1887.

Synonyms: — See BASSLER 1938 (p. 85).

Regional distribution: — France (Lower Ordovician), ? Japan (Lower Ordovician), USSR and Estonia (Middle Ordovician), Canada (Middle and Upper Ordovician), Bohemia (Middle and Upper Ordovician), Scotland (Middle and Upper Ordovician), Sweden (Lower Silurian), Germany (Lower Devonian).

Stratigraphic range: — Lower Ordovician — Lower Devonian.

#### **Dendrocystites** sp.

Pl. 2, fig. 9.

1907 Cystoideenstiel. — WIMAN 1907 b, p. 14, Pl. 2, fig. 7.

Locality: — Hulterstad, Öland (boulder).

Stratum: — Dense, grey, siliciferous limestone: West-Baltic Leptaena limestone, probably lowest Silurian.

Material: — An imperfect stem-fragment, RM Ec 4192.

Description: — A small fragment, length 3 mm and greatest width about the same. Some ten plates of different size and outline are visible. In the state here described the fossil unfortunately represents only the half of the specimen figured by WIMAN, as reveals a comparison with WIMAN's figure. So half the fossil, indeed very fragmentary already when reproduced by WIMAN, must have been lost by injury in some way or other.

Remarks: — In discussing the nature of the present fossil-fragment, WIMAN (1907 b, p. 14) suggested that it may possibly represent the peduncle of a cirriped, but with regard to the irregular arrangement of the plates and their structure he would rather look upon it as a "Cystoideenstiel, etwa wie bei *Dendrocystites Sedgwicki*". Further reference was made to BARRANDE

1887, Pl. 27, fig. 10. According to the opinion of the present writer there is no doubt as to its belonging to the echinoderms, the fractures of the plates showing the crystalline cleavage typical of echinoderms (cf. yet p. 48 above). And the resemblance between our specimen and part of the figure referred to by WIMAN is so great that we may safely label it as *Dendrocystites*. It is true that the crystalline cleavage is also seen in certain species of *Lepidocoleus* (cf. WITHERS 1926, p. 84). Yet the specimen cannot be identified with any species of *Lepidocoleus*, nor with any other machaerid (in speaking of cirripeds WIMAN probably had in view such forms as are now called Machaeridia).

A specific determination would, however, be too hazardous. As just mentioned, the specimen RM Ec 4192 recalls indeed rather strongly BARRANDE's figure 10 of *Dendrocystites sedgwicki* BARRANDE, excepting *D. rossicus* JAEKEL the only species of the genus known at the time WIMAN's paper was published. BATHER (1913, p. 374, fig. 8) divided the stem of *Dendrocystites* into three regions: — the proximal (next to the theca), median, and distal. Our specimen represents the transitory portion between the proximal and the median regions. To judge from the figures delivered by BARRANDE (1887, Pl. 26; Pl. 27, figs. 2—4, 6—18) and BATHER (1913, Pl. 1, figs. 5—7; text-fig. 8) this portion of the stem is generally in *Dendrocystites sedgwicki* considerably broader and consists of a greater number of plates than is the case in the present specimen. The same appears from a few imprints of Bohemian specimens [RM Ec 5538, 5542], from Zahořany (d 3—d 4, Upper Llandeilian—Lower Ashgillian), available to the writer. In the search for a species with which our specimen could be compared in the first hand we have of course to look for a form with corresponding stratigraphic appearance. Besides *Dendrocystites sedgwicki* the following species have been described: — from Bohemia *D. barrandei* (BATHER 1913) (d 2, Middle Llandeilian); France *D. vidali* THORAL 1935 (Upper Tremadocian); Scotland *D. scoticus* (BATHER 1913) (Drummuck Group, Ashgillian); Germany *D. globolus* DEHM 1934 (Lower Devonian); USSR and Estonia *D. rossicus* JAEKEL 1900 (Vaginatum limestone, Upper Arenigian),<sup>1</sup> *D. kuckersianus* HECKER 1940 (Kukruse and Itfer, Upper Llandeilian); Canada *D. (?) paradoxicus* (BILLINGS 1859) (Trenton, Lower Caradocian), *D. sagittarius* (THOMAS & LADD 1926)<sup>2</sup> (Richmond, Ashgillian), "Stems of *Dendrocystites* or of

<sup>1</sup> JAEKEL (1900, p. 673) and BATHER (1913, p. 396, § 152) gave as horizon for this species the "Brandschiefer" (Kukruse, Upper Llandeilian). According to HECKER (1940 b, p. 65) this statement may be false.

<sup>2</sup> For this species THOMAS & LADD (1926, p. 6) erected the new genus *Iowacystis*. BATHER (1928 a, p. 5) found it "plain that the species is a *Dendrocystis*" (the same statement he had made already in 1926 in his review in Geol. Zbl. 34, abstr. 662, of the paper of THOMAS & LADD. DEHM (1934, p. 21) would prefer to rank *Iowacystis* at least as a subgenus of *Dendrocystites*.

some allied group" were further reported by KOBAYASHI (1934, p. 525) from Korea (Asaphellus zone, Tremadocian).

Of the species listed above, which might represent all the forms described as yet, *Dendrocystites scoticus* and *D. sagittarius* are those which come next to the Swedish specimen with regard to age. None of these seems, however, to have very close affinities to it, nor is any of the other species identical, though in general appearance some of them may remind of it. So, as was already emphasized, we have better not give any specific name to this fragment. Yet a certain interest is attached to this isolated find of a *Dendrocystites* within the Swedish area.

### Order **Mitrata** JAEKEL 1918.

#### Family **Anomalocystitidae** (MEEK) BASSLER 1938.

Genus *Ateleocystis* LINDSTRÖM 1888, non *Ateleocystites* BILLINGS 1858.

H. WOODWARD (1871, 1880) endeavoured to show that *Anomalocystites* HALL 1859 and *Placocystites* DE KONINCK 1869 were to be looked upon as synonyms of *Ateleocystites*, a view which could not be corroborated by subsequent authors. SCHUCHERT (1904, p. 205) remarked that *Ateleocystites*, which was figured very poorly by BILLINGS (1858, p. 73), is not well known but that the genera mentioned seem to be distinct.

#### *Ateleocystis huxleyi* LINDSTRÖM 1888, non BILLINGS.

1888 *Ateleocystis Huxleyi* BILLINGS. — LINDSTRÖM 1888 b, p. 20.

Remarks: — The species was recorded in a faunal list and thus not made known by any description. It was to be expected that the specimen, or the specimens, on which the statement was based should be found in the collections of the State Museum of Natural History of Stockholm. But unfortunately the present author did not succeed to find any specimens which could be suspected to be the fossil alluded to by LINDSTRÖM.

As to the species listed by LINDSTRÖM we can safely state that it was not conspecific with *Ateleocystites huxleyi* BILLINGS, which is an Ordovician form, from the Trenton of Canada, whereas LINDSTRÖM's species was recorded from a much higher stratigraphic horizon, viz. some part of the Silurian of Gotland. It was said to originate from the division c of LINDSTRÖM's stratigraphic table. This division being no stratigraphic unity (cf. HEDE 1921, pp. 12, 24),<sup>3</sup> the place in the Silurian series of strata of the

<sup>3</sup> HEDE, J. E., 1921. Gottlands silurstratigrafi. — Sver. Geol. Unders. Ser. C. 305. Stockholm.



form discussed remains undecided. Very likely we can leave *Ateleocystites* in a restricted sense out of account, the genus being monotypical and thus only represented by the Trenton species.<sup>4</sup> LINDSTRÖM was undoubtedly acquainted with WOODWARD's papers quoted above. As we have seen, that author included in *Ateleocystites* the genera *Anomalocystites* HALL and *Placocystites* DE KONINCK. As far as known, the former genus is restricted to the American Lower Devonian (cf. SCHUCHERT 1904, p. 206)<sup>5</sup> and thus not very likely to have occurred in the Silurian of Gotland. *Placocystites*, finally, with the unique species *P. forbesianus* DE KONINCK, has been met with in English Wenlockian beds.<sup>6</sup> A related genus, *Placocystella*, was lately made known by RENNIE (1936), from the Bokkeveld series (Lower Devonian) of South Africa. Another Lower Devonian genus, which is said to come close to *Placocystites*, is *Rhenocystis* DEHM 1933, from Bundenbach, Germany.

Summing up what has now been said of the several genera joined by WOODWARD into *Ateleocystites*, and of other more or less related forms, we arrive at the conclusion, that the Gotland form referred to by LINDSTRÖM 1888 might have been a species of *Placocystites*.<sup>7</sup>

### Class **Edrioasteroidea** BILLINGS 1858 (1854), emend. BATHER 1899.

Synonyms: — See BATHER 1900, p. 205, and BASSLER 1935, p. 2.

The year of publication of the class-name should possibly be 1854, which could unfortunately not be checked, since the paper of BILLINGS 1854 was not available to the present writer. But according to SPRINGER (1913, p. 158) BILLINGS in 1854 only "called attention to the great difference between the forms now grouped under this name [Edrioasteroidea] and the typical

<sup>4</sup> By accident RENNIE (1936, p. 274) gave the age of *Ateleocystites* as early Devonian.

<sup>5</sup> Four species of "*Anomalocystites*" were described by BARRANDE 1887 from the Ordovician of Bohemia. As BATHER (1900, p. 51) pointed out these are doubtful. JAECKEL 1900 considered "*A.* *bohemicus*" not determinable (p. 668) and referred "*A.* *incipiens*" to a new genus, *Mitrocystella* (p. 672). In 1918 the same author erected the genus *Lagynocystis* for "*A.* *pyramidalis*" (p. 121) and *Anomocystis* for "*A.* *ensifer*" (the last-mentioned name is preoccupied by *Anomocystis* HAECKEL 1896, used for *Anomalocystites* HALL).

<sup>6</sup> A form from the British Wenlock described by HAECKEL (1896, p. 42, Pl. 2, fig. 12) as *Atelocystis gegenbauri* is undoubtedly conspecific with *Placocystites forbesianus*.

*Placocystis africana* REED 1925, from the Lower Devonian of South Africa, based on a very imperfect specimen, according to RENNIE (1936, p. 274) has to be removed from *Placocystites*.

<sup>7</sup> When the manuscript was ready for the press this deduction was confirmed in so far as the author was told by Prof. GISLÉN that LINDSTRÖM's specimen had been handed over earlier to him for examination. According to kind information by Prof. GISLÉN this specimen represents a new species of *Placocystites*, related to *P. forbesianus*.

Cystideans, and in 1858 [BILLINGS 1858 b, p. 85] suggested that they should be arranged as a suborder to be called Edrioasteridae". Anyhow, it is not correct to write, as did BASSLER (1935, p. 2; 1936, p. 2), "BILLINGS, 1854—58". The error might have arisen from BATHER's reference, within the same brackets in which the year of publication was given, to other concerned papers by authors using the term Edrioasteroidea ["Edrioasteroidea, E. BILLINGS (1854, —58; HUXLEY, 1877; and BATHER, 1899)"].

With regard to the branched ambulacra present in the genus *Thresherodiscus* (FOERSTE 1914 (p. 432), the diagnoses of authors have to be modified so as to exclude the demand for unbranched ambulacra.

A dividing into orders was not undertaken by BASSLER 1935 and 1936, nor does the writer think it wise here to introduce any on the basis of the limited number of genera represented in Sweden.

### Family *Stromatocystitidae* BASSLER 1936.

Genus *Stromatocystites* POMPECKJ 1896, emend. SCHUCHERT 1919.

Genotype: — *Stromatocystites pentangularis* POMPECKJ 1896.

Synonyms: — *Stromatocystis* BATHER 1899, 1900; SPRINGER 1913; ZITTEL-BROILI 1924.

Regional distribution: — Newfoundland (Lower Cambrian), ?Sweden (Lower Cambrian), Bohemia (Middle Cambrian), France (Middle Cambrian).

Stratigraphic range: — Lower—Middle Cambrian.

### *Stromatocystites balticus* JAEKEL 1899.

Text-fig. 26.

1899 *Stromatocystites balticus*. — JAEKEL, p. 42, Pl. 2, fig. 7.

1918 *Stromatocystites balticus* JAEKEL. — JAEKEL, p. 112, text-fig. 104: A.

Holotype: — A specimen from the collection of C. GOTTSCHÉ, Hamburg, referred to by JAEKEL 1899; actual depository unknown to the present writer; the specimen figured by JAEKEL 1899, deposited in the Breslau collection, was said to be preserved only in the state of a gutta-percha cast, on account of which it cannot be considered the holotype (cf. RICHTER 1943, pp. 370—371).<sup>1</sup>

Type locality: — Unknown, the specimens being collected from erratics, which must, however, be supposed to have originated from Öland or some subaqueous Cambrian area of the Baltic.

<sup>1</sup> RICHTER, R., 1943. Der nomenklatorische Typus. — Z. Deutsch. Geol. Gesellsch. **95**, Berlin.

**Type stratum:** — Sandstone from the stage of *Paradoxides paradoxissimus* ("*P. tessini*"), Middle Cambrian.

**Material:** — No specimen available to the present writer; according to JAEKEL 1899 (p. 42) two specimens are known.

**Diagnosis:** — A species of *Stromatocystites* with indistinctly differentiated and weakly calcified, coriaceous skeleton, with small marginal plates.

**Remarks:** — Having no specimen of this species at his disposal, the present author can add nothing to the meagre description given by JAEKEL and reproduced in the above diagnosis. So no comparison with congeneric species will be undertaken.

The first species made known, *Stromatocystites pentangularis* POMPECKJ, the genotype, originates from the Middle Cambrian of Bohemia. In 1905 MIQUEL (pp. 476, 482) recognized as a species of *Stromatocystites* a form which he had before (MIQUEL 1894, p. 10) referred to as "*Trochocystites cannati*", from the Middle Cambrian of Hérault, France. The position of this species seems questionable. According to informations received by THORAL (1935 b, p. 35) from STUBBLEFIELD and SPENCER, *Stromatocystites cannati* is probably identical with a form from the Middle Cambrian of Hérault, mentioned by JAEKEL 1923 (p. 344) as "*Cambraster* n. g." and interpreted as an asteroid. In 1919, finally, SCHUCHERT reported a new species, *Stromatocystites walcotti*, and var. *minor*, from the Lower Cambrian of western Newfoundland. These are all species known to science.

JAEKEL (1899, p. 42) proposed that "die meist fünftheiligen, als *Medusites Lindströmi* aus dem unteren Cambrium (sog. Eophyton-Sandstein) Schwedens von LINNARSSON und NATHORST beschriebenen Steinkerne nach Form und Grösse vielleicht die Innenausfüllung von Stromatocystiden bilden könnten". His proposal was repeated by MACBRIDE (1906, p. 596). It was already mentioned above (p. 10) that *Medusina costata* (TORELL) (= "*Medusites lindströmi*" LINNARSSON), from the Lower Cambrian Mickwitzia sandstone of Västergötland, was described as "*Agelacrinus? Lindströmi*" by LINNARSSON (1871 a, p. 12). According to the opinion of the present writer, NATHORST was undoubtedly right when denying (in 1881, cf. p. 10 above, foot-note 9) the echinoderm nature of the fossils in question. Specimens kept in LM examined by the author do not show the slightest trace of a pavement of plates or scales nor of an anal pyramid or a pore-system. Moreover, all specimens available to the author (9) are tetradial, this form of development thus certainly being quite as common as the quinqueradial type. So there is nothing to indicate the proposed belonging to the Edrioasteroidea of these fossils.



Text-fig. 26. *Stromatocystites balticus* JAEKEL. Nat. size. (From JAEKEL 1918, fig. 104: A).

In the explanation of Pl. 2 of his memoir of 1899, JAEKEL located *Stromatocystites balticus* without reserve to "Schweden", in 1918 (p. 112, text of fig. 104 A) particularized as "Südschweden". Provided the surrounding rock is Paradoxissimus sandstone, the specimens, if originating from exposed strata, must have come from Öland, which is the only area of Sweden characterized by Middle Cambrian sandstone facies.

### Family *Cyathothecidae* JAEKEL 1927.

The family was established (JAEKEL 1927 b) to receive the genera *Cyathotheca* JAEKEL 1927 and *Cyathocystis* F. SCHMIDT 1879 (in ZITTEL 1879).

### Genus *Cyathotheca* JAEKEL 1927.

Genotype: — *Cyathotheca suecica* JAEKEL 1927.

Diagnosis: — A genus of *Cyathothecidae* with irregular, goblet-shaped and attached theca, closed above by 5 interradian plates, beside which is placed the separate anal opening.<sup>2</sup>

Regional distribution: — USSR (Middle Ordovician), Sweden (Upper Ordovician or Lower Silurian).

Stratigraphic range: — Middle—Upper Ordovician (or Lower Silurian).

### *Cyathotheca suecica* JAEKEL 1927.

Pl. 1, fig. 6. Text-fig. 27.

1927 *Cyathotheca suecica*. — JAEKEL 1927 b, p. 2, Pl. 1, figs. 1, 2, 3, 3 a.

Holotype: — RM Ec 2305.<sup>3</sup>

Type locality: — Not known with certainty; probably Boda (NW of the church), Dalarna.

Type stratum: — Red marl-shale, probably embedded in the Boda limestone, Upper Ordovician or Lower Silurian.<sup>4</sup>

<sup>2</sup> Translated from JAEKEL 1927 b (p. 4).

<sup>3</sup> The box to contain JAEKEL's holotype of *Cyathotheca suecica* was empty when received from the State Museum of Natural History, as was also stated on an accompanying label. The specimen RM Ec 2305, which was immediately recognized as the lost holotype of *Cyathotheca suecica*, was found in another box, on the bottom of which is written in the hand of JAEKEL: — "interessanter Stielansatz. Jkl." There might be no doubt as to the identity of the holotype, though for some reason or other the measurements given by JAEKEL are constantly inferior to those stated in RM Ec 2305 by the present writer.

<sup>4</sup> Of *Cyathotheca* may possibly also be true what was said above (p. 191, foot-note 3) about *Tormoblastus*, as was kindly pointed out by Dr P. THORSLUND (letter to the author).



**Material:** — One unique specimen, the holotype.

**Diagnosis:** — A species of *Cyathotheca*, the theca of which has subparallel sides and irregularly lobate lower surface, being produced laterally into a point of attachment in the anal (V—I) interradius.

**Description:** — There is not very much to be added to JAEKEL's description (1927 b) of this species but for the sake of completeness a full account will be given here.

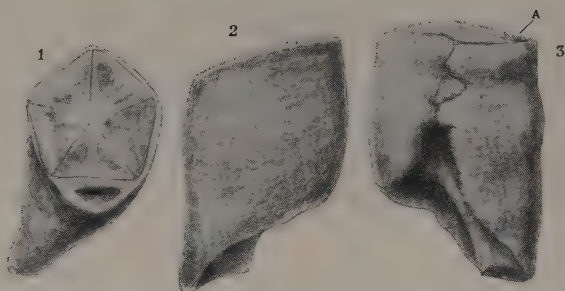
**General shape of the theca.** Theca small-sized, goblet-shaped, decidedly pentagonal at the adoral surface, if we exclude the separately placed anus. The lower surface of the theca is, as mentioned in the diagnosis, very irregularly developed. The theca is slightly curved to the left when looked at from behind.

**Measurements.** Greatest height of the theca 7 mm (JAEKEL gave 6 mm). The diameter of the adoral surface measured along the anal plane 4.6 mm (JAEKEL 4 mm), the diameter transverse to it 3.6 mm (JAEKEL 3 mm).

**Thecal skeleton.** With regard to the differentiation of the skeleton, *Cyathotheca suecica* is exceedingly simple. No more than six pieces are namely to be recognized, by far less than in any other echinoderm, as remarked JAEKEL (1927 b, p. 2), who also pointed out that some further pieces, forming an anal pyramid, may be supposed to have been present.

The walls of the theca are formed, as it seems, by one sack-like piece. If consisting of several plates, these are completely amalgamated. Taking its origin at the edge of the adoral surface there is a bulging line running in radius II towards the base of the theca (cf. text-fig. 27: 3). Whether this is a suture may be an open question. Two more vertical lines are visible, one of them running approximately in radius I and the other in radius III. These are undoubtedly secondary fissures in the stereothek, however. — No marginal plates are present.

The adoral surface has a pentagonal portion, very slightly elevated over the edge of the thecal wall, and a separate lunate portion, lying in the inter-radius V—I. The pentagonal surface is covered by 5 interrarial triangular valvulae, forming a very depressed pyramid. JAEKEL supposed that these plates correspond to the *OO* of *Cyathocystis* rather than to the innermost (interrarial) ambulacrals. The sutures between the *OO* and the wall-cover are rather distinct, whereas the limits between the *OO* mutually are exceedingly obscure. They are no doubt correctly represented, however, in text-fig. 27: 1. Here appear also, though not very clearly, the peculiar dendroid marks interpreted by JAEKEL as crystallographic limits of lattice-structure visible through the transparent *OO* (see also Pl. 1, fig. 6 a). They are decidedly not sutures between plates. Instead they are to be considered phenomena caused by secondary infiltration of some mineral solution. — As mentioned above, the lunate surface is devoid of any traces of covering plates.



Text-fig. 27. *Cyathotheca suecica* JAEKEL, holotype [RM Ec 2305]. 1 Actinal view. 2—3 Right and left lateral views.  $\times 5$  (approx.). — Dalarna: Boda (?). (From JAEKEL 1927 b, Pl. 1).

No surface structures of stereom are present, the theca being all over smooth and polished. It gives the impression of being considerably worn.

**Ambulacral system.** The ambulacral grooves are not visible though undoubtedly present between and below the *OO*, which serve thus at the same time as covering plates of the grooves, no ambulacrals being developed. The ambulacra are confined to the adoral surface. *Brachioles* and *hydropore* are not present.

**Alimentary canal.** The mouth, lying in the centre of the ambulacra, is also covered by the *OO*. The anus is located to the lunate space between the thecal wall and the base of *O 1*. It is a rather big lunate opening.

No *gonopore* was observed.

The surface of attachment is very irregularly lobated. It can hardly be decided whether the specimen was attached to some organism or to some detrital object. As for the confamiliar *Cyathocystis plautinae* F. SCHMIDT, which in conformity to *Cyathotheca* is devoid of "rhizoids", its author proposed it to be a parasitic form (F. SCHMIDT 1880, p. 5), since it had always been found to grow on monticuloporids. HECKER (1928, pp. 74—75) observed specimens (on hydrophorids) having no connexion whatever with monticuloporids. So he concluded that it is simply a case of epicy, being neither parasitic nor symbiotic, *Cyathocystis plautinae* only using the stocks of monticuloporids or the thecae of hydrophorids as a substratum because it had no means to attach itself to the unfastened sea-floor. Likely we have to imagine the same for *Cyathotheca*.

**Discussion:** — One more species of *Cyathotheca* is known, viz. *C. corallum* (JAEKEL 1918), from the Vaginatum limestone of the Leningrad district. It is slightly bigger than *C. suecica* and rather similar to it, but the theca is pronouncedly ceratoid with a pointed surface of attachment. The actinal region is not known closely. The species was re-figured by JAEKEL (1927 b, Pl. 1, figs. 4—6), who also recorded affinities and differences between the two genera *Cyathotheca* and *Cyathocystis*.

**Regional distribution:** — *Cyathotheca suecica* has been found hitherto only in Dalarna, Sweden. The locality of the holotype, which is the only specimen known to the writer, was mentioned above. In a review of JAEKEL's paper 1927 b,<sup>5</sup> BATHER said he had collected specimens from various localities of the Siljan district. Probably these are in the British Museum, London.

**Stratigraphic range:** — Upper Ordovician or Lower Silurian.

### Family Hemicystitidae BASSLER 1936.

#### Genus *Pyrgocystis* BATHER 1915.

**Genotype:** — *Pyrgocystis sardesoni* BATHER 1915.

**Synonym:** — *Scalpellum* AURIVILLIUS 1892, non LEACH.

**Diagnosis:** — A genus of Hemicystitidae with high subcylindrical or polygonal, turret-shaped theca composed of scale-like plates imbricating from below upwards; adoral surface with five broad, straight ambulacra.

**Regional distribution:** — USSR (Middle Ordovician), N. America (Middle Ordovician, Upper Silurian), Scotland (Upper Ordovician), England (Middle Silurian), Sweden (Middle Silurian), Germany (Lower Devonian).<sup>6</sup>

**Stratigraphic range:** — Middle Ordovician—Lower Devonian.

**Remarks:** — The organization of this peculiar genus was not understood until the appearance of the study of BATHER (1915 a), performed on a material containing specimens with the adoral surface preserved. The Swedish forms referred to *Pyrgocystis* were originally described by AURIVILLIUS (1892) as cirripeds. They were revised by BATHER in the paper just mentioned, where also two British and one American species were described. Further contributions to the knowledge of the genus were delivered by RUEDEMANN (1925), RICHTER (1930), and HECKER (1939).

The following analytical table includes all species of *Pyrgocystis* hitherto made known.

- 1 (2). Turret octagonal in transverse section. . . . . *P. octogona* RICHTER.
- 2 (1). Turret subcircular in transverse section.
- 3 (4). Alternating tiers of turret plates; 22 columns of plates . . . . . *P. sardesoni* BATHER.
- 4 (3). Alternating tiers of turret plates; 8—10 columns of plates.

<sup>5</sup> Geol. Zbl. 35. Leipzig 1927. Abstr. 919.

<sup>6</sup> JAEKEL (1927 b, p. 4) said he was going to increase the knowledge of the "Pyrgocystidae" by describing "eine anscheinend sehr primitive neue Form aus Norwegen". The intended paper was never published, and we do not know whether the Norwegian form alluded to belongs to *Pyrgocystis* or to some related genus.

- 5 (14). Overlap of plates moderate, the number of exposed margins of plates per 3 mm (in vertical direction) being less than 7.<sup>7</sup>
- 6 (11). Number of exposed margins of plates per 3 mm, (3—) 4—6.
- 7 (10). 8 columns of plates.
- 8 (9). Columns of plates separated by faint grooves ..... *P. procera* (AURIVILLIUS).
- 9 (8). Columns of plates inosculating ..... *P. varia* (AURIVILLIUS).
- 10 (7). 10 columns of plates ..... *P. grayae* BATHER.
- 11 (6). Number of exposed margins of plates per 3 mm, 2—3; columns closely inosculating.
- 12 (13). Turret cylindrical ..... *P. cylindrica* (AURIVILLIUS).
- 13 (12). Turret conical ..... *P. pulkovi* HECKER.
- 14 (5). Overlap of plates considerable, the number of exposed margins of plates per 3 mm, 7—11 (or even more).
- 15 (22). 8 columns of plates.
- 16 (19). Exposed margin of plates parabolic; grooves between columns of plates deep.
- 17 (18). Number of exposed margins of plates per 3 mm, 7 .. *P. batheri* RUEDEMANN.
- 18 (17). Number of exposed margins of plates per 3 mm, 8—9 *P. ansticei* BATHER.
- 19 (16). Exposed margin of plates forming an arc of a circle.
- 20 (21). Number of exposed margins of plates per 3 mm, 7—9; grooves between columns of plates well marked *P. sulcata* (AURIVILLIUS).
- 21 (20). Number of exposed margins of plates per 3 mm, 9—11; grooves between columns of plates inconsiderable; [alternatively 9 columns of plates] ..... *P. volborthi* HECKER.
- 22 (15). 9 columns of plates.
- 23 (24). Grooves between columns of plates well marked .... *P. gracilis* HECKER.
- 24 (23). Grooves between columns of plates inconsiderable; [alternatively 8 columns of plates] ..... *P. volborthi* HECKER.

As to the Swedish forms, an impartial examination indicated that BATHER's revision of the species had to be modified. This is no wonder, indeed, if we consider that BATHER (as he declared, 1915, p. 5) could not study the Swedish material directly, owing to the dangerous state of the North Sea, but had to base his opinion of these very intricate fossils on the description and the figures of AURIVILLIUS (1892). To-day, thirty years later, the same force majeure hinders the present writer from gaining personal knowledge of the species dealt with by BATHER but this drawback is compensated by BATHER's excellent working up the material.

Only in the conception of one of the Swedish species, *Pyrgocystis cylindrica*, the author agrees fully with BATHER. *Pyrgocystis sulcata*, on the other hand, has been subject to the greatest change in its extension. All species listed by BATHER as synonyms of *P. sulcata* have been removed and

<sup>7</sup> The very basal tiers should be excluded when taking the measurements.



referred to other species. *Pyrgocystis varia* has been ranked as a separate species. Further *Pyrgocystis procera*, which according to BATHER had no synonyms, has been thought to comprise *Scalpellum procerum*, *S. strobiloides*, *S. granulatum*, and *S. fragile*, all of AURIVILLIUS. The reasons for this new arrangement might be evident from the analytical table above and will be further considered in describing the several species.

***Pyrgocystis sulcata* (AURIVILLIUS 1892).**

Pl. 1, fig. 7. Pl. 2, fig. 1.

- 1841 Columnae Crinoidis fragmentum. — HISINGER 1841 a, p. 4, Pl. 41, fig. 6 [the figure is inverted].  
 1892 *Scalpellum sulcatum*. — AURIVILLIUS, p. 13, Pl.-fig. 11.  
 1915 *Pyrgocystis sulcata* AURIVILLIUS sp. (ex parte). — BATHER 1915 a, p. 58.

**Holotype:** — RM Ec 6091.

**Type locality:** — Djupvik (Djauvik), Eksta, Gotland.<sup>8</sup>

**Type stratum:** — Mulde marl, Middle Silurian.<sup>9</sup>

**Material:** — About 50 specimens, RM.

**Diagnosis:** — A species of *Pyrgocystis* with theca slightly tapering basalwards, its diameter in the upper region being nearly half of its total height; turret plates in tiers of 4 plates, which alternate regularly, forming 8, (usually) distinct columns separated by well-marked grooves; number of exposed margins of thecal plates, 7—9 per 3 mm (measured vertically); exposed margin of plates forming an arc of a circle.

**Description:** — General shape of the theca. The theca has the shape of a turret, subcircular in transverse section and slightly tapering basalwards. It may be slightly curved or about straight, obviously an adaptation conditioned by the varying consistence or configuration of the substratum (BATHER 1915 a, p. 57, supposed that the theca "stuck in the ooze, but may possibly have been attached to seaweeds").

**Measurements:** — (it should be noted that all specimens available are incomplete, the adoral region being preserved in no instance).

<sup>8</sup> According to verbal information by Dr HEDE, the fossils of older collections labelled "Djupvik, Eksta" originate probably to a great extent from the stretch of coast 1 km NE of the fishing-village Djupvik, parish of Eksta. The exposure has the name "Blåhäll" in the geol. map-sheet Hemse (Sver. Geol. Unders. Ser. Aa. 164, Stockholm 1927).

<sup>9</sup> According to HEDE 1942, p. 20 (On the correlation of the Silurian of Gotland. — Lunds Geol. Fältklubb 1892—1942, Lund 1942; also Meddelanden fr. Lunds Geol.-Min. Inst. 101), "it appears probable that the Mulde marl lies at the top of the Wenlockian, and that it corresponds in age to the *Cyrtograptus lundgreni* zone of the British sequence. Yet the possibility that it forms transitional beds from Wenlockian to Ludlovian cannot be neglected altogether".

| (Measurements in mm)        | RM Ec 6091<br>(holotype) | RM Ec<br>6092 a | RM Ec<br>6092 b | RM Ec<br>6092 c | RM Ec<br>6092 d  | RM Ec<br>6092 e |
|-----------------------------|--------------------------|-----------------|-----------------|-----------------|------------------|-----------------|
| Height of the theca . . . . | 10                       | 10.2            | 10.1            | 9.8             | 9.3              | 7.4             |
| Diameter at upper end . .   | $4.7 \times 4.1$         | 4.4             | 4.1             | 4               | $5.7 \times 4.6$ | 2.9             |
| Diameter at basal end . .   | $3.5 \times 3.1$         | 3.6             | 3.2             | 3.2             | $4.2 \times 3.4$ | 2.3             |

**Thecal skeleton.** As mentioned, only the subactinal region of the theca is known. It is covered by scale-like plates, arranged in regularly alternating tiers of 4 plates in each tier. In this way the plates come to stand in 8 series or columns, separated by grooves, which are usually quite distinct. In the holotype there are some 45 tiers composing the theca. The mutual overlap of the plates in a column is — as is always the case in *Pyrgocystis*, though more or less pronounced — so considerable that the shape of the separate plates cannot be determined, but for the basal-most plates forming the termination of the theca. These are closely amalgamated so as to form a sort of ferrule. All basal plates are not equally high; they seem to reach a maximum height of 2 mm. But it may not be taken for granted that the remaining plates are in detail similar to those of the basal tier. And in fact, a longitudinal section reveals that the total length of a plate may amount to 3 mm, whereas the exposed upper margin has an average height of 0.4 mm only. The width of the thecal plates is in the upper region of the holotype about 1.2 mm. Basalwards the width is somewhat diminished in connexion with the general tapering of the theca. The average width: height ratio (of a whole plate) is 0.4. The whole of the visible portion of each plate is about securiform, its upper outline having generally the shape of an arc of a circle. The plates, which are slightly convex, are set at an angle of about  $30^\circ$  towards the vertical axis, which varies, however, a little within different portions of the theca. This is also true of the width of the lumen contained within the thecal walls. It approaches more or less one-third of the diameter of the turret.

**Surface structures of stereom** do not seem to be remarkable in any way, the plates being almost smooth.

The ambulacral system as well as the openings of the alimentary canal, and other eventual exits remain unknown in consequence of the imperfect state of preservation of the actinal region of all specimens available.

The basal surface of the theca is more or less flattened, often somewhat excavated or furnished with small excavations, very likely reproducing the surface of the substratum to which the organism was attached. This does not confirm BATHER's proposition quoted above that the theca stuck in the ooze.

**Discussion:** — It was mentioned already in the introductory remarks on *Pyrgocystis* that the different forms of AURIVILLIUS' genus *Scalpellum* regarded by BATHER as belonging to *Pyrgocystis sulcata* must be removed, for reasons which will be explained in discussing the several species to which they have been referred here.

The fossil figured by HISINGER (1841 a, Pl. 41, fig. 6) and mentioned as "Columnae Crinoidis fragmentum — Gottlandia" seems to have been lost since it could not be found in the HISINGER collection of the State Museum. It is so characteristic, however, that it can safely be referred to *Pyrgocystis sulcata*.

In general appearance the present species reminds us very much of the English species *Pyrgocystis ansticei* BATHER, Wenlock shale (Middle Silurian). Their interrelations were dealt with thoroughly by BASSLER (1915 a, p. 51 seq.). The main differences are that in *Pyrgocystis ansticei* the free margins of the plates are parabolic and the overlap of the plates still more pronounced.

The North American *Pyrgocystis batheri* RUEDEMANN (Bertie waterlime, Salinan, lower part of Upper Silurian) comes also very close to our species. The American species seems to differ by having very deep grooves between the columns of plates and often parabolic outline of the exposed margin of the plates. The plates were described as thick (0.3 mm), smooth or of very finely granular surface (RUEDEMANN 1925, p. 39).

Two species from the lower part of the Middle Ordovician of the Leningrad district, *Pyrgocystis volborthi* HECKER and *P. gracilis* HECKER were said to display some resemblance to *P. sulcata* (HECKER 1939, pp. 245—246). In the first-mentioned one the number of exposed margins of plates per unit of measure is greater, and the grooves between the columns of plates are weakly defined. The surface of the plates is finely and densely granulated. In *P. gracilis* there are (as also alternatively in *P. volborthi*) nine columns of plates, the plates are arranged more densely and have a somewhat tapering margin.

**Regional distribution:** — Sweden, Gotland: Djupvik.

**Stratigraphic range:** — Uppermost Wenlock (or basal Ludlow).

### *Pyrgocystis procera* (AURIVILLIUS 1892).

Pl. 2, figs. 2—6.

1892 *Scalpellum procerum*. — AURIVILLIUS, p. 18, Pl.-fig. 15.

1892 *Scalpellum granulatum*. — AURIVILLIUS, p. 16, Pl.-figs. 20—22.

1892 *Scalpellum strobiloides*. — AURIVILLIUS, p. 17, Pl.-figs. 17—19.

1892 *Scalpellum fragile*. — AURIVILLIUS, p. 19, Pl.-fig. 10.

1915 *Pyrgocystis procera* AURIVILLIUS sp. — BATHER 1915 a, p. 59.

1915 *Pyrgocystis sulcata* AURIVILLIUS sp. (ex parte). — BATHER 1915 a, p. 58.

**Holotype:** — RM Ec 6110.

**Type locality:** — Visby ("Vattenfallet")?, Gotland.

**Type stratum:** — ? Upper Visby marl, Lower Silurian.<sup>10</sup>

**Material:** — Some 20 specimens, RM.

**Diagnosis:** — A species of *Pyrgocystis* with theca very slightly tapering basalwards, its diameter in the upper region being about two and a half of its total height; turret plates in tiers of 4 plates, which alternate regularly, forming 8 columns separated by not very distinct grooves; number of exposed margins of thecal plates 4—6 per 3 mm (measured vertically); exposed margin of plates forming more or less an arc of a circle.

**Description:** — General shape of the theca. The theca has largely the same shape as that of the preceding species but is tapering less remarkably. The turret is subcircular in transverse section and may be fairly straight or slightly curving.

**Measurements** (as in *P. sulcata* the adoral region is missing in all specimens available; it should also be noted that the very base of the holotype is not preserved).

| (Measurement in mm)           | RM Ec 6110<br>(holotype) | RM Ec<br>6103    | RM Ec<br>6098 a | RM Ec<br>6093 a | RM Ec<br>6093 b | RM Ec<br>6093 c  |
|-------------------------------|--------------------------|------------------|-----------------|-----------------|-----------------|------------------|
| Height of the theca . . . . . | 10.6                     | 5                | 11              | 10.6            | 10.2            | 9                |
| Diameter at upper end ..      | 3.5                      | $2.3 \times 1.5$ | $3.8 \times 3$  | 3.4             | 2.5             | $3.7 \times 3.5$ |
| Diameter at basal end ..      | 3                        | 2                | $2.5 \times 2$  | 3.2             | 2.4             | 3.2              |

RM Ec 6103 is AURIVILLIUS' holotype of *Scalpellum fragile* from Djupvik, Eksta, Gotland (Mulde marl). The specimen might be a juvenile form. It is somewhat compressed in the proximal region.

RM Ec 6098 a is from Fröjel, Gotland (Mulde marl). RM Ec 6093 a—c originate from Djupvik.

RM Ec 6111, the holotype of *Scalpellum strobiloides* AURIVILLIUS (Mulde, Mulde marl) has a height of 11.6 mm. It is strongly compressed; therefore no measurements of its diameter can be given. The holotype of *Scalpellum granulatum* (RM Ec 6106) is also imperfect and compressed.

**Thecal skeleton.** The actinal region is not preserved in any specimen available. The turret-shaped theca is covered by scale-like plates in alternating tiers of 4 plates in each tier. The 8 columns of plates thus produced are separated by rather vague grooves. In this species, as well as

<sup>10</sup> In the oldest label accompanying the holotype, the locality is given thus: — "Wisby vattenfallet", the second word being appended in another hand (probably by C. WIMAN). If the statements on the label can be trusted, then — according to kind information by Dr HEDE — the attached traces of matrix and the colour of the fossil indicate that it must have come from the Upper Visby marl (Upper Valentian).



in those described below, the plates do not overlap so closely as in *Pyrgocystis sulcata*. On that account a spiral arrangement of the plates is also conspicuous. The same feature was recognized by HECKER in his species *Pyrgocystis volborthi*. HECKER (1939, p. 245) said that the spiral arrangement had never been observed before and that it might possibly be proper to some other species of *Pyrgocystis* as well. In point of fact, however, it was described and analysed several years before by BATHER (1915 a, pp. 52—53).

In the holotype there are about 25 tiers of plates. In other specimens referred to *Pyrgocystis procera* the number varies according to the length of the preserved portion of the theca. Per 3 mm measured vertically there are 4—6 exposed margins of plates. The upper outline of each plate forms more or less an arc of a circle but is often somewhat irregular or nearly straight. All of the exposed portion of a plate is in several instances tolerably rhomboidal (or, sometimes, triangular). The shape of the separate plates is, of course, not visible in consequence of the overlap. Their total length — measured in longitudinal sections — is about 2.3 mm; the height of the exposed portion of the same plates is about 0.8 mm; the width of certain plates of the same specimen [RM Ec 6111], in the region where the measurements just given were obtained, is about 2 mm. As may appear from the figures of different specimens of this species, there is, however, a rather considerable variation with regard to the shape of the exposed portion of the plates. The average width: height ratio (of a whole plate) is 0.9. In some specimens this ratio is not valid for the plates of the basal tier, these plates having a relatively greater height. This is true especially of specimens referred by AURIVILLIUS to *Scalpellum granulatum*.

In the specimen RM Ec 6111 the plates of the upper region are set at an angle of about  $20^{\circ}$  towards the vertical axis. The plates nearer to the base are directed more outwards. This character was mentioned by AURIVILLIUS (1892, p. 17) in his description of *Scalpellum strobiloides*. It is also met with in the specimen figured by AURIVILLIUS as *Scalpellum fragile*. BATHER (1915 a, p. 54), referring to the conditions in *Pyrgocystis ansticei*, pointed out that no weight can be attached to the difference in direction of the plates at the distal end. In the specimen RM Ec 6093 d of *Pyrgocystis procera* here figured (Pl. 2, fig. 2) no such difference is apparent.

On *Scalpellum procerum*, AURIVILLIUS (1892, p. 18) remarked that the plates are slightly bent on their vertical axes so as to give the columns a keeled appearance. The feature mentioned cannot be said, however, to be specific of this very species. On the contrary it is to be found in specimens of most species of *Pyrgocystis*, reaching its extreme development in the Lower Devonian *Pyrgocystis octogona* RICHTER. — A secondary thickening of the plates was observed by AURIVILLIUS (1892, pp. 17, 19) for his species *Scalpellum strobiloides* and *Scalpellum fragile*.

Surface structures of stereom are usually not remarkable, the plates being almost smooth. Only in specimens referred by AURIVILLIUS to *Scalpellum granulatum* the surface is very finely granulated. This ornament — as pointed out BATHER 1915 a, p. 54 — might have no specific importance but be due to better preservation.

The ambulacral system as well as the apertures of the alimentary canal and other eventual exits are unknown as yet, no complete specimen being available.

The basal surface of the theca is not preserved in many specimens but seems to have the same character as that of *Pyrgocystis sulcata*.

Discussion: — In *Pyrgocystis procera*, in the sense of the present writer, four species of AURIVILLIUS' *Scalpellum* were joined. The "species" in question were thought to be conspecific, having very much the same arrangement and development of the thecal plates and differing in no essential respects as far as the author is aware. BATHER (1915 a, p. 59) recognized *Pyrgocystis procera* as a separate species, but *Scalpellum fragile*, *Scalpellum strobiloides*, and *Scalpellum granulatum*, the two last-mentioned, though, with a mark of interrogation, were listed as synonyms of *Pyrgocystis sulcata*. They are, however, as just mentioned, not separable from *Scalpellum procerum*, whereas this group of forms, constituting *Pyrgocystis procera*, seems to be delimited sufficiently from *Pyrgocystis sulcata*: — the overlap of plates is considerably smaller, and the grooves separating the columns of plates are decidedly less distinct than in the last-mentioned species. Of greater importance is that the shape of the plates also seems to be a different one, the width: height ratio being in *Pyrgocystis procera* approximately 0.9, in *P. sulcata* 0.4.

Otherwise there is no close affinity between this and any other species of *Pyrgocystis* except *Pyrgocystis varia* (cf. below in the discussion of that species).

Regional distribution: — Sweden, Gotland: Visby?, Mulde, Djupvik.

Stratigraphic range: — ? Upper Valentinian—Wenlock (or basal Ludlow).<sup>11</sup>

### *Pyrgocystis varia* (AURIVILLIUS 1892).

Pl. 1, fig. 7.

1892 *Scalpellum varium*. — AURIVILLIUS, p. 15, Pl.-figs. 12—14.

1915 *Pyrgocystis sulcata* AURIVILLIUS sp. (ex parte). — BATHER 1915 a, p. 58.

Holotype: — RM Ec 6104.

Type locality: — Djupvik (Djauvik), Eksta, Gotland.

<sup>11</sup> Cf. p. 205, foot-note 9.

**Type stratum:** — Mulde marl, Middle Silurian.

**Material:** — 9 specimens, most of them very imperfect (a few specimens can hardly be determined safely). [RM].

**Diagnosis:** — A species of *Pyrgocystis* with theca steadily tapering basalwards, its diameter in the upper region being one-half or more of its total height; turret plates in tiers of 5 plates, which alternate regularly so as to form 8 columns of plates closely inosculating; number of exposed margins of thecal plates (3—)4(—5) per 3 mm (measured vertically); exposed margin of plates forming an arc of a circle.

**Description:** — General shape of the theca. As in the preceding forms the theca of this species has the shape of a turret, sub-circular in transverse section, steadily tapering basalwards more conspicuously than in the species described above. The specimens available are all tolerably straight or very slightly curved.

**Measurements** of the holotype. Height 8.2 mm, diameter at upper end 4.5 mm, diameter at basal end 2.8 mm. The other specimens are too imperfect to supply reliable measurements.

**Thecal skeleton.** The actinal region is not preserved in any specimen. The theca is covered by plates in alternating tiers of 4 plates in each tier. The 8 columns of plates thus produced are closely inosculating. Owing to the relatively inconsiderable mutual overlap of the thecal plates a spiral arrangement is also clearly visible.

In the holotype there are 14 tiers of plates. The exposed margins are (3—)4(—5) per 3 mm measured vertically. Their upper outline is in the holotype forming a regular arc of a circle. The exposed portions of the plates are securiform in the upper portion of the theca and triangular basalwards. The total height of the plates — measured in a longitudinal (polished) section of the holotype — is about 3.5 mm, whereas the height of the exposed portion varies between 1.5 and 0.6 mm. The width is about 2 mm, thus giving a width: height ratio (of a whole plate) of about 0.6. The plates of the basal tier do not diverge remarkably in shape from those covering the rest of the theca; in many specimens of the species described above the basal-most plates are rather aberrant as we have seen. The position of the plates is also a different one, being in the basal region very close to the vertical line; certain plates of the upper region, on the other hand, form an angle of about  $45^\circ$  towards the vertical axis.

The plates are gently bent along their median lines but are in no way keeled.

**Surface structures of stereom** are not prominent, the plates being almost smooth or very finely granulated.

The **ambulacral system** as well as the apertures of the **alimentary canal** and other eventual exits are unknown as yet, no complete specimen being available.

The basal surface of the theca seems to be almost flat.

**Discussion:** — The present species differs from *Pyrgocystis sulcata* by a number of characters, of which only the inconsiderable overlap of plates and the close inosculation in lateral direction may be mentioned. With regard to the width: height ratio of the individual plates, *Pyrgocystis varia* holds an intermediate position between *Pyrgocystis sulcata* and *Pyrgocystis procera* (0.4—0.6—0.9). It has a certain affinity to the last-mentioned species but differs also by the lack of longitudinal grooves separating the columns of plates; the number of exposed margins of plates per unit of measure is usually smaller. In the shape of plates it has some resemblance to *Pyrgocystis cylindrica* but differs i.a. by its conical shape of the theca (cf. also the discussion of *P. cylindrica* below).

Of species from foreign countries *Pyrgocystis pulkovi* HECKER displays a very great resemblance indeed to our species, as observed HECKER (1939, p. 246). The shape of the turret is the same; the degree of overlap is also about the same and the plates are closely inosculating. The Russian Ordovician species was said to differ in outline of the exposed margins of plates, which is rounded and slightly tapering. It may also be noted that the width of plates is somewhat greater in *Pyrgocystis pulkovi* according to the data communicated by HECKER.

**Regional distribution:** — Sweden, Gotland: Djupvik.

**Stratigraphic range:** — Wenlock (or basal Ludlow).

### *Pyrgocystis cylindrica* (AURIVILLIUS 1892).

Pl. 2, fig. 8.

1892 *Scalpellum cylindricum*. — AURIVILLIUS, p. 18, Pl.-fig. 16.

1915 *Pyrgocystis cylindrica* AURIVILLIUS sp. — BATHER 1915 a, p. 59.

**Holotype:** — RM Ec 6109.

**Type locality:** — Visby ("Vattenfallet")?, Gotland.<sup>12</sup>

**Type stratum:** — ? Upper Visby marl, Lower Silurian.

**Material:** — 1 specimen only, the holotype.

**Diagnosis:** — A species of *Pyrgocystis* with theca very slightly tapering basalwards<sup>13</sup> when looked at from a certain aspect and almost cylindrical after turning the theca on its vertical axis at an angle of 90° towards the aspect mentioned before; the diameter in the upper region being a little more than one-third of its total height; turret plates in tiers of 4 plates, which alternate regularly, so as to form 8 columns of plates closely in-

<sup>12</sup> As in the case of the holotype of *Pyrgocystis procera*, the locality "Vattenfallet" is appended on the label in another hand (C. WIMAN's?); cf. p. 208, foot-note 10.

<sup>13</sup> It is to be noted that the very base is not preserved.



osculating; number of exposed margins of thecal plates 2(—3) per 3 mm (measured vertically); upper outline of exposed portion of plates being a pointed arch.

**Description:** — **General shape of the theca.** The theca is almost cylindrical when looked at from certain directions but slightly tapering when seen from other aspects. This is due to the different shape of a transverse section in the upper region and in the basal region: — in the former it is almost circular (or very slightly octagonal), in the latter it is oval. The turret is almost straight.

**Measurements** of the holotype. Height 9 mm, diameter at upper end 3.2 mm, diameter at basal end  $3 \times 2.5$  mm.

**Thecal skeleton.** The actinal region is lacking as in the preceding species. The theca is covered by plates in alternating tiers of 4 plates in each tier. The 8 columns of plates thus produced are closely inosculating. A spiral arrangement of the plates is also very prominent in consequence of the slight mutual overlap of plates.

The theca consists of 12 tiers of plates only, but it should be remembered that it is imperfect at either pole. In a space of 3 mm measured vertically there are as a rule 2 margins exposed. The upper margin of each plate forms a pointed arch. All of the exposed portion of a plate has the shape of a rhomboid. The total height of the plates is not known, since the unique specimen could not be sacrificed for the preparing of slides. The average height of the exposed portion of the plates is 1.5 mm, for the distal-most plates preserved, a little more; the width is about 2 mm, a little more or a little less. The plates rest closely against each other and might not diverge very much in position from the vertical axis.

The plates are bent gently on their median line. In some instances there is an indication of a median ridge produced into a short point.

**Surface structures of stereom** are not conspicuous in other respects, the plates being almost smooth.

The **ambulacral system** as well as the apertures of the **alimentary canal** and other eventual exits remain unknown until complete specimens will be available.

The **basal surface** of the theca is not preserved.

**Discussion:** — With regard to the general shape of the theca this species has to be compared in the first hand with the Swedish *Pyrgocystis procera* and the American Lower Ordovician *Pyrgocystis sardesoni* BATHER. The last-mentioned species is well separated already by having the thecal plates arranged in 22 columns. In *Pyrgocystis procera* the columns of plates are separated by grooves, very faint though, whereas in the present species the plates are closely inosculating. Considering the shape of the separate plates, the greatest affinity seems to be with *Pyrgocystis pulkovi* HECKER, in which

the exposed portion of each plate is rounded and slightly tapering in outline. But in the Russian species the theca is pronouncedly conical and the relative width of the plates is somewhat greater. The number of plates per unit of measure is about the same, possibly the overlap is a little greater in *Pyrgocystis pulkovi*. *Pyrgocystis varia* also offers several features recalling the species under discussion. It differs, however, in the following points: — the theca tapers more conspicuously; the mutual overlap of plates is somewhat greater; exposed margins of plate form an arc of a circle, not being pointed as in *Pyrgocystis cylindrica*.

Regional distribution: — Sweden, Gotland: Visby?

Stratigraphic range: — ? Upper Valentinian.

In typical development the four Swedish species of *Pyrgocystis* here maintained are clearly separable from each other by characters prominent enough. But in cases — and especially if we have to deal with fragmentary or in other ways ill-preserved specimens — it might be a hard task to perform a reliable determination. This, however, is a predicament in which the paleontologist is often brought on the examination of a critical fossil material.

There is, indeed, a great difference between *Pyrgocystis cylindrica*, probably appearing in the Upper Valentinian, and the younger *Pyrgocystis sulcata*, probably Wenlockian of age. If only these two species should be taken into consideration, you would be disposed to recognize certain trends in the evolution of the genus with regard to the development of the theca and its skeleton elements: — transition from a tolerably cylindrical theca to a tapering one; from inosculating plates in spiral arrangement to plates in distinct columns separated by grooves; from vertical to oblique position of the plates; from a moderate overlap of plates to densely crowded plates, i.e. an evolution towards greater plasticity of the theca without loss of its firmness. The other two species are not to be inserted, however, in this hypothetical evolutionary line. *Pyrgocystis varia*, in several respects displaying a great resemblance to *P. cylindrica*, which was supposed to represent the primitive stage, is namely confined to the same stratum as the supposed end-form. On the other hand, *P. procera*, which approaches to *P. sulcata*, appeared contemporaneously with *P. cylindrica*. The environmental conditions were undoubtedly similar for the several species. It must be said, therefore, that obvious trends do not seem to have guided the development within the genus *Pyrgocystis*.

It should also be noted that the Ordovician *Pyrgocystis* stock of the Leningrad district was differentiated very much in the same way as the Silurian *Pyrgocystis* assemblage of Gotland, so as to include contemporaneous representatives of the morphologic extremes placed at each end-point of the arbitrary evolutionary line.

## Incertae sedis.

Order **Cyclocystoidea** MILLER & GURLEY 1895.Family **Cyclocystoididae** S. A. MILLER 1882.Genus ***Cyclocystoides*** SALTER & BILLINGS 1858.

Genotype: — *Cyclocystoides halli* BILLINGS 1858 (in SALTER & BILLINGS).

**Diagnosis:** — A genus of Cyclocystoididae with the submarginal ossicles of the lower plate differentiated (in upper face) into a proximal portion, vaulted and granulated, with concave inner margin, and a distal portion, excavated tangentially and containing a few (more or less mamillary) elevations; the vaulted portion pierced by pores equal in number to the elevations.

**Discussion:** — FOERSTE (1920 b, p. 59 seq.) tried to separate the known forms of *Cyclocystoides* by introducing the new genera *Narrawayella* and *Savagella* for those species that were thought not to coincide with typical species of *Cyclocystoides*. Of the two genera proposed, *Savagella* (genotype: — *Cyclocystoides ornatus* SAVAGE 1917) might be distinct. It differs from *Cyclocystoides* in having the large (submarginal?) ossicles grooved radially instead of granulated and with vertical inner face instead of concave. The mamillary elevations were said to be lacking (FOERSTE 1920 b, p. 61). For *Narrawayella*, however, the present writer has some doubts as to its validity. The specimens which were referred there are in general so poorly preserved that it might not be possible to recognize their structures safely. The large (submarginal?) ossicles were described by FOERSTE as cuneate and coarsely pitted, bearing no distal elevations. To this may be said that in species referred to *Cyclocystoides* also the submarginal plates are regularly more or less distinctly wedge-shaped. In worn specimens the surface ornament is not visible, and the same may be the case of the distal elevations. Moreover, in lower face the structures mentioned do not, of course, appear and the outline of the ossicles is cuneate. The author is not sure if not the forms referred by FOERSTE to *Narrawayella* represent lower plates in lower view. For these reasons the writer is not inclined to accept *Narrawayella* as a separate genus until further evidence of its validity has been presented.

**Regional distribution:** — N. America (Middle and Upper Ordovician), Scotland (Upper Ordovician), England (Lower and Middle Silurian), Sweden (Middle Silurian), Belgium (Lower Devonian).

**Stratigraphic range:** — Middle Ordovician—Lower Devonian.

*Cyclocystoides lindströmi* n. sp.

Pl. 15, figs. 7—8. Text-figs. 28—29.

1888 *Cyclocystoides* sp. — LINDSTRÖM 1888 b, p. 20.

**Derivation of name:** — The species is named in honour of the eminent paleontologist G. LINDSTRÖM (1829—1901), who recognized *Cyclocystoides* in the Silurian of Gotland.<sup>1</sup>

**Holotype:** — RM Ec 5028. The specimen was cut along a diameter and a polished section prepared from the one piece. Further it was broken tangentially along an existing breakage line in order to make the inner parts of the submarginal area accessible for study.

**Type locality:** — Visby, Gotland.

**Type stratum:** — Probably some basal layer of the Höglint group, Middle Silurian.<sup>2</sup>

**Material:** — 5 more or less fragmentary specimens [RM Ec 5028—5032] are available. Two of these [RM Ec 5029 and 5031] show the lower face of the lower plate. In RM Ec 5029 the central disk is almost entirely destroyed; about a third of the ossicles of the submarginal ring is lacking. In RM Ec 5031 nothing is visible with the exception of submarginal plates when looked at from above. After preparing a polished section cutting radially through one of the ossicles, part of the central disk also came to view (in radial section). The other three specimens, which are thought to show the interior of the lower plate, are less imperfect and in a better state of preservation.

**Diagnosis:** — A species of *Cyclocystoides* perfectly circular in outline; diameter of the central disk of the lower plate of the holotype 40 mm; submarginal area of about 40 tolerably uniform ossicles, each of which has regularly 2 rounded protuberances distally.

**Description:** — The central disk, which is flattened or slightly convex, seems to be made up of a frame of radiating rays, probably disposed in more than one layer. The number of rays could not be ascertained but might distally be twice that of submarginal ossicles. The rays originate from the centre of the disk; by successive bifurcation their number is

<sup>1</sup> The old labels accompanying the specimens of *Cyclocystoides* in the State Museum are written by LINDSTRÖM.

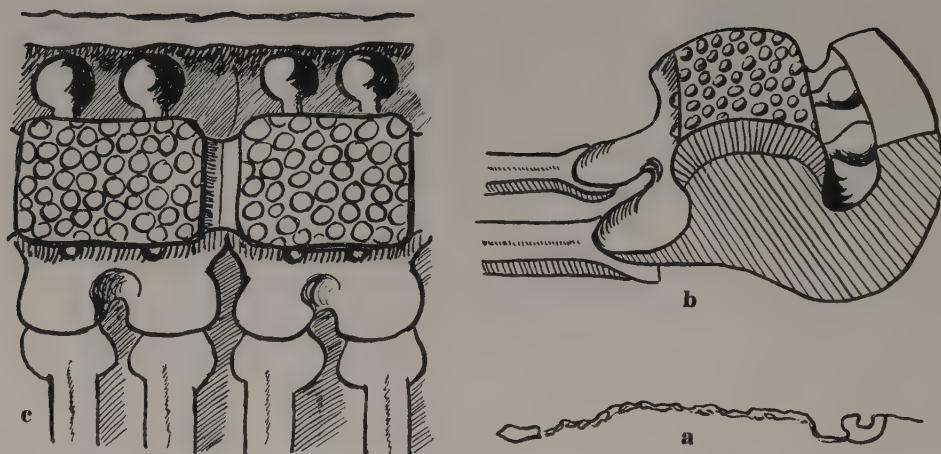
<sup>2</sup> In the old label there is no information of the stratum from which the specimen was collected. Dr HEDE was so kind as to examine the sample containing the fossil. According to verbal information by Dr HEDE, the sample is very likely to originate from some basal layer of the Höglint group (=lower part of Wenlock). Most of the associated forms (*Heliolites* sp., *Halysites* sp., and other Anthozoa; Bryozoa; Brachiopoda; *Beyrichia* sp.) are not very decisive. Some fragments of *Plectodonta* cf. *duvali* (DAVIDSON) were detected, however. This species is confined to the horizon mentioned.



increased distally. Each ray is divided medially by a faint groove and connected with adjacent rays by short anastomoses. By this the central disk obtains a reticulate appearance. The rays seem to have been solid. No definite apertures could be traced in the central disk. It is true that in RM Ec 5032 there is a small subcentral depression, and in the holotype there is an eccentric depression, but undoubtedly neither of these are primary structures. In the figure of *Cyclocystoides salteri* HALL delivered by HALL (1872, Pl. 6, fig. 16; reproduced with slight modifications by BATHER 1900, p. 211) an oval eccentric opening is indicated to represent the mouth. BATHER (1900, p. 211) interpreted it as anus and also spoke of "a central pyramid of minute plates (mouth?)", which was observed already by HALL (1872, p. 218), who did not, however, give any opinion of its nature. The structures mentioned have not been confirmed by subsequent investigators, nor by the present writer.

The submarginal area contains invariably 39—40 ossicles, somewhat wedge-shaped, forming a ring around the central disk. As far as could be recognized, the inner margin of the ossicles overlap slightly the adjacent rays of the central disk. A similar observation was made by FOERSTE (1924, p. 81) for *Cyclocystoides illinoisensis* MILLER & GURLEY.<sup>3</sup> The ossicles are fairly equal-sized, but a few do not reach the average size but are a little narrower in lateral direction. Each ossicle is differentiated in a rather complicated way. Its shape might appear from the slightly diagrammatic representations in text-fig. 28 a, b. In unweathered specimens the interior portion of the ossicles, up to the edge of the tuberculated vault, is covered by the elements of the central disk. In its distal portion each ossicle is excavated so that a canal is formed running around the disk distally of the vaulted inner portions of the ossicles. Invariably, as it seems, two mamillary elevations are contained in the groove of each ossicle. Each knob tapers proximally so as to be connected with the vault by a small duct. Several authors (MILLER & DYER 1878, pp. 33, 34, 35; BEGG 1934, p. 222) stated that the ducts penetrate the vaults radially to open on the — likewise excavated — inner side of the ossicles. The same observation can be made in the holotype of the present species. The ducts, as observed BEGG (l.c.), continue in radial direction below the surface of the disk. The proximal portion of the ossicles — that hidden by the central disk — is divided into two laps. If well preserved, the ossicles of our species are seen to be strongly

<sup>3</sup> According to FOERSTE (1920 b, pp. 62—63), MILLER & GURLEY's fig. 28 on Pl. 5 (1895) very likely represents a species identical with *Savagella ornata* (SAVAGE), whereas the name *Cyclocystoides illinoisensis* should be restricted to forms resembling their fig. 27. That species was supposed to belong to a separate genus, for which no name was proposed, however. The number of submarginal ossicles was said not to exceed 20, contrary to the statement in the original description.



Text-fig. 28. *Cyclocystoides lindströmi* n. sp., holotype [RM Ec 5028], lower plate. a Section along a diameter; nat. size. b Isolated ossicle of the submarginal zone in lateral view;  $\times 8$  (approx.). c Two ossicles of the submarginal zone seen from above;  $\times 8$  (approx.). — Gotland: Visby.

tuberculated on the upper surface of the vault, whereas laterally they are bevelled and striated vertically on their upper border. The same features have been observed previously in different species. RAYMOND (1913, p. 26) pointed out that the vertical striations of the ossicles indicate “cartilaginous or muscular attachments between the plates, giving considerable flexibility to the ring”, which is undoubtedly true.

RAYMOND (l. c.) further stated that the canal containing the mamillary elevations was covered with small plates, which according to FOERSTE (1924, p. 81) could be moved at will for the entrance or outlet of water. These covering plates could not be recognized definitely in our specimens, nor is the marginal zone of “sinuous threads or possibly of imbricating plates” (BEGG 1934, p. 222) present in certain species previously described to be observed.

In the specimens showing the lower face of the lower plate, the ossicles of the ring are smooth, wedge-shaped (especially in RM Ec 5031, cf. text-fig. 29).

#### Measurements:

| (Measurements in mm)                                                            | RM Ec 5028<br>(holotype) | RM Ec<br>5029 | RM Ec<br>5030 | RM Ec<br>5032 |
|---------------------------------------------------------------------------------|--------------------------|---------------|---------------|---------------|
| Diameter of central disk .....                                                  | 40                       | 30            | 42            | 43            |
| Average radial extension of exposed<br>portion of ossicles of submarginal area  | 5                        | 4             | 5             | 4             |
| Average lateral extension of exposed<br>portion of ossicles of submarginal area | 5                        | 2.7           | 3.9           | 3.2           |

About half of the radial extension of the submarginal ossicles is occupied by the tuberculated vault.



Text-fig. 29. *Cyclocystoides lindströmi* n. sp. [RM Ec 5031]. Lower face of ossicles of the submarginal zone in the lower plate.  $\times 2$ . — Gotland: Visby.

**Discussion:** — From *Cyclocystoides insularis* n. sp. described below, the species under consideration is well separated by its size and the different development of the ossicles of the submarginal area. The only species hitherto described attaining a diameter comparable to that of our form, is *Cyclocystoides huronensis* BILLINGS 1865 (redescribed and figured adequately by RAYMOND 1913, p. 29, Pl. 3, fig 2, and by FOERSTE 1924, p. 80, Pl. 6, fig. 3), from the Upper Ordovician (Hudson River) of Rabbit Island, Lake Huron, Canada (also reported from the Richmond, Upper Ordovician, of W Ontario, by FOERSTE 1916 b, p. 126). At a diameter of the central disk of about 35 mm, the holotype of that species show 59 submarginal ossicles, each of which with one or two mamillary elevations. *Cyclocystoides halli* BILLINGS 1858 (in SALTER & BILLINGS), from the Middle Ordovician (Trenton) of Canada, comes rather close to *Cyclocystoides lindströmi* with regard to the shape of the submarginal ossicles, which have two mamillary elevations. These, however, seem to be considerably more extended in radial direction than is the case in our species. The number of submarginal ossicles is 30—35 and the diameter of the central disk, to judge from the figures of RAYMOND 1913 (Pl. 3, figs. 1, 3, 4), not reaching 20 mm. In the original description (BILLINGS in SALTER & BILLINGS 1858, p. 86), however, it was said to be "one or two inches".

The remaining North American species, all of them Ordovician, are considerably smaller, so far as known, and have a considerably smaller number of submarginal ossicles. This is also true of the Upper Ordovician (Ashgillian) Girvan species *Cyclocystoides decussatus* BEGG 1934, which also differs by several other features. The Lower Silurian (Upper Llandoveryan) *Cyclocystoides davisii* SALTER 1858 (in SALTER & BILLINGS), from Presteign, S. Wales, has 48—49 submarginal ossicles and shows eight rays only in the centre of the disk; its diameter is not known to the writer. Finally, according to MAILLIEUX 1926, BATHER noted the genus in Wenlockian deposits of Britain. This species (or maybe there are several species), which is thus more or less homotact with the species from Gotland, has not been described as yet, nor has the Lower Devonian species from Belgium announced by MAILLIEUX 1926.<sup>4</sup>

**Regional distribution:** — Sweden, Gotland: Visby, Gnisvärd.

**Stratigraphic range:** — Lower Wenlock.

<sup>4</sup> After the decease of BATHER in 1934, the Lower Devonian specimen was handed over to H. SIEVERTS[-DORECK] for description (N. Jb. f. Mineral. 1934. Ref. 3, p. 626).

*Cyclocystoides insularis* n. sp.

Pl. 15, fig. 9. Text-fig. 30.

**Derivation of name:** — From Lat. *insula*, island, the only specimen available having been collected in the island of Fårö, NE of Gotland.

**Holotype:** — RM Ec 5033.

**Type locality:** — Fårö, probably the northern coast, closer locality unknown.

**Type stratum:** — Höglint group(?).<sup>5</sup>

**Material:** — One unique specimen, the holotype.

**Diagnosis:** — A species of *Cyclocystoides* oval in outline; long diameter of the central disk of the holotype 9 mm, short diameter 7 mm; submarginal area of 24 largely equal-sized ossicles, 8 of which have 2 mamillary elevations distally and 16 of which have 3 protuberances of that kind, each ossicle with 2 elevations being flanked at each side by two ossicles bearing 3 distal elevations.

**Description:** — The central disk has been entirely removed by uncaredful preparation by an earlier student of the specimen. As mentioned, it was oval, the short diameter being about 78 per cent of the long one.

The submarginal area is made up of 24 ossicles, which are about equal-sized but differentiated in two kinds of somewhat different shape. In point of principle they might be constructed in the same way as in the preceding species. But whereas in *Cyclocystoides lindströmi* each ossicle has two distal mamillary elevations, there are in the present species certain ossicles bearing three protuberances. In fact there are twice as many ossicles of the last-mentioned kind. The two types of ossicles alternate regularly in the submarginal ring so that each ossicle with two elevations has at each side two ossicles with three elevations. If we prefer to express this case in a formula, it could be written "n×8". In this formula "n" corresponds to the term  $\begin{bmatrix} 3 & 3 & 2 \\ 1 & 1 & 1 \end{bmatrix}$ , in which the "numerators" indicate the number of mamillary elevations of each of three ossicles following each other. It is obvious that there are also other possibilities for arranging the ossicles into terms.

The ossicles of the submarginal area are slightly wedge-shaped. Their average width is 1.2 mm. The average measure of their extension in radial direction is 2.2 mm, of which the vaulted portion occupies about 1.3 mm.

<sup>5</sup> As is evident from the surrounding rock, this specimen cannot possibly derive from any horizon older than the Höglint group or younger than the Slite group. Probably it originates from the Höglint limestone at the north-coast of Fårö (verbal information by Dr HEDE).



If this portion was tuberculated cannot be ascertained, for the specimen is rather considerably worn. Nor are lateral striae visible. The ossicles make the impression of having been more closely connected mutually in lateral direction than is the case in e.g. *Cyclocystoides lindströmi*. The shape of the distal protuberances is also a different one. They are namely distinctly elongate, having their long axis in radial direction. They seem to be intimately connected by their bases with the vaulted portion of the ossicles without an intermediary duct as in the species described above. It may be presumed, however, that those elevations were connected with the interior of the central disk by canals penetrating the vaults of the submarginal ossicles in a similar way as was observed for *Cyclocystoides lindströmi* and other forms, though in the present specimen it could not be stated.

The marginal zone is partly preserved. Its structure cannot be made out safely, but it seems to consist of a series of more or less vertical plates, each facing one of the distal elevations of the submarginal ossicles. Outside the vertical plates there is a narrow zone of threads or indistinct plates. The breadth of the marginal zone seems hardly to reach 1 mm.

**Discussion:** — The present species, which might be tolerably synchronous with the other Swedish form known, differs clearly from it by its minor size and, especially, by the different shape of the ossicles of the submarginal area. Among other Silurian species, of which data are available, *Cyclocystoides davisii* SALTER 1858 (in SALTER & BILLINGS), from the Upper Llandovery of S. Wales, has double the number of submarginal ossicles. The Lower Devonian species reported from Belgium (MAILLIEUX 1926) is not described as yet.

Of North American Ordovician species, partly based on very poor specimens, there are several of about the same size as *Cyclocystoides insularis* and with a moderate number of submarginal ossicles. One species, *Cyclocystoides (Narrawayella) nitidus* FABER 1886, from the Upper Ordovician (Maysville) of Transit, Ohio, has, at a diameter of the central disk of 7 mm, 24 submarginal ossicles as in our species. The specimen was in no good state of preservation, and the figure delivered by FABER (1886, Pl. 1, fig. 1) does hardly permit a closer comparison. The species seem to be rather similar, however. *Cyclocystoides illinoisensis* MILLER & GURLEY 1895 is also badly preserved but was said to have 24—30 submarginal ossicles. No measurements were given, but the species was stated to be large. "The outer part or margin of the rim bears four or five rows of [transversally] elongated nodes, such as have not, we believe, been heretofore found on any specimen" (MIL-



Text-fig. 30. *Cyclocystoides insularis* n. sp., holotype [RM Ec 5033]. Portion of the marginal and submarginal zones of the lower plate seen from above.  $\times 8$ . — Gotland: Fårö.

LER & GURLEY 1895, p. 61). This species — from the Upper Ordovician (Hudson River) of Illinois — has obviously no strong affinities to the species under discussion.<sup>6</sup> — MILLER & DYER (1878, p. 32 seq.) described several forms from the Upper Ordovician (Cincinnati group) of Ohio. A few of these (*Cyclocystoides minus*, *C. parvus*, *C. mundulus*, referred by FOERSTE 1920 b to *Narrawayella*) present themselves as rings of worn submarginal ossicles showing no details. Size and number of ossicles were taken as specific characters. The lowest number of ossicles (19) is found in the smallest "species" (*minus*, about 5 mm),<sup>7</sup> the greatest number (32) in the largest form (*mundulus*, about 6.5 mm). Intermediate both regarding number of submarginal ossicles (26) and size (about 6 mm) is *C. parvus*. This correlation between size and number of submarginal ossicles may indicate that the three "species" mentioned represent growth stages of one species, all the more so as they were obtained from the same horizon and locality (Morrow, Ohio). It seems rather likely that the number of submarginal ossicles may have varied within certain limits in one and the same species, the definite number of the adult being acquired gradually. Immature specimens, therefore, may have less submarginal ossicles than are characteristic of the adult.

A safer base for delimiting different species might be the shape of the ossicles of the submarginal area. As we have seen, there is in *Cyclocystoides insularis* a remarkable regularity in the alternation between ossicles bearing two distal elevations and such bearing three. This was expressed by the formula  $n \times 8$ , in which  $n$  corresponds to the term  $\begin{bmatrix} 3 & 3 & 2 \\ 1 & 1 & 1 \end{bmatrix}$  (cf. above). For *Cyclocystoides magnus* MILLER & DYER 1878 the analogous formula would be — according to data communicated by MILLER (1881, p. 70) —  $n \times 5$ , where  $n = \begin{bmatrix} 3 & 3 & 2 & 2 \\ 1 & 1 & 1 & 1 \end{bmatrix}$ . This tells us that in the species mentioned (Upper Ordovician, Hudson River, Ohio) there are 20 submarginal ossicles of two different types: such with 2 distal elevations and such with 3, being grouped into pairs alternating with each other.<sup>8</sup> The Ashgillian species *Cyclocystoides decussatus* BEGG, from Girvan, Scotland, has the formula  $[n \times 5] + 2$ , where  $n = \begin{bmatrix} 3 & 3 & 3 & 2 & 2 & 2 \\ 1 & 1 & 1 & 1 & 1 & 1 \end{bmatrix}$ . The formula means that the species has 32 submarginal ossicles developed and arranged as expressed by the term  $n$  and that there is some irregularity in the scheme of alternation caused by two "super-numerary" ossicles. — Two more species, that show some similarity to

<sup>6</sup> Cf. p. 217, foot-note 3.

<sup>7</sup> The measurements refer to the diameter of the central disk.

<sup>8</sup> As figured by MILLER & DYER 1878, Pl. 2, figs. 8, 8 a, the species has certain ossicles bearing four distal elevations.

*Cyclocystoides insularis*, have to be mentioned, viz. *Cyclocystoides bellulus* MILLER & DYER 1878, from the Upper Ordovician (Cincinnati group) of Cincinnati, and *Cyclocystoides salteri* HALL 1866, from the Middle Ordovician (Trenton) of Canada. The former, at a diameter of about 10 mm, has probably 18 submarginal ossicles, each with two, three, or four mamillary elevations; their mode of alternation is unknown. The ossicles are strongly tuberculated on the vault and with vertical striae laterally. The latter species has a diameter of about 11 mm and two or three mamillary elevations to each of the submarginal ossicles, 26 in number. From the figure of HALL 1872 (Pl. 6, fig. 6) a system in the arrangement of the submarginal ossicles is not apparent; maybe it is not accurately drawn.

The above discussion indicates that *Cyclocystoides insularis* does not show a close affinity to any species hitherto described.

Regional distribution: — Sweden: Fårö.

Stratigraphic range: — Lower Wenlock.

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The present writer has no facts to add to the assumptions of previous investigators regarding the physiology of *Cyclocystoides*. We must imagine that some sort of water circulation has taken place. In the specimens studied by the author, the mamillary elevations do not seem to be penetrated by any pores beyond those connecting them with the interior of the central disk. Yet it must be supposed that water was let in into the circular canal in which the mamillary elevations are situated, passed into those, and proceeded in radial direction into the central disk. The mamillary elevations cannot have been facets of brachioles, as supposed by H. SIEVERTS 1934 (cf. above p. 45), nor is there anything to indicate that they were bases of spines. Both theories are made impossible by the fact that the canal, in which they are located, was evidently roofed over by small movable plates (cf. above p. 218). It is astonishing, indeed, that no openings of the alimentary and reproduction system have been recognized. It is true that RAYMOND (1913, p. 28) claimed to have observed a central plate of a specimen proposed by FOERSTE (1920 b, p. 60) to be named *Narrawayella raymondi*. BEGG (1934, pp. 223—224) rejected on theoretical grounds the thought of a location of the anus to the lower side of the ventral part, but declared at the same time that in the specimen studied by him there is no evidence of an orifice in the covering dorsal plate. As for propositions made by HALL (1872) and BATHER (1900), cf. above p. 217.

In the case of *Cyclocystoides*, there are many obscure points. Unfortunately we have for the present only to call attention to the fact and to acknowledge our deficient information of the organization of the genus.

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### Addendum

to *Heliocrinites variabilis* n. sp., p. 137, line 10 from below:

R e g i o n a l d i s t r i b u t i o n : — Sweden, Dalarna: Boda, Kallholn, Lissberg, Osmundsberg, Skålberget.

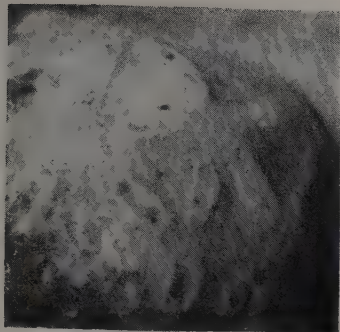
S t r a t i g r a p h i c r a n g e : — Boda limestone, Upper Ordovician and (or) Lower Silurian.



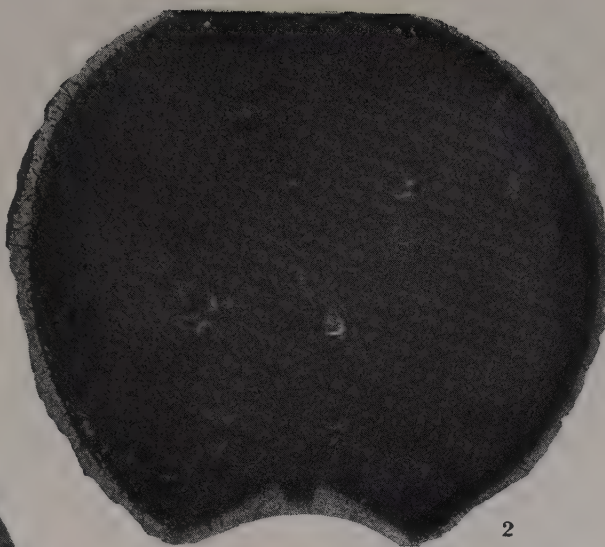


## PLATES

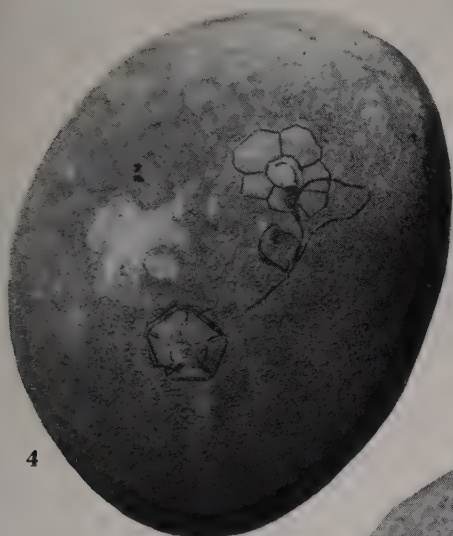




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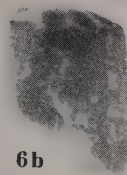
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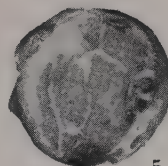
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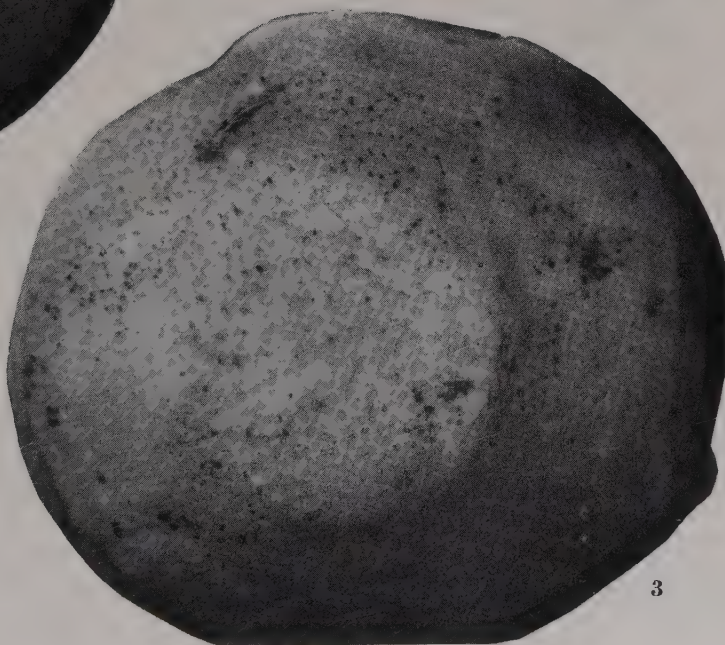
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6b



5



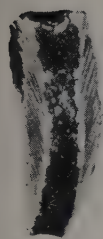
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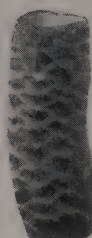




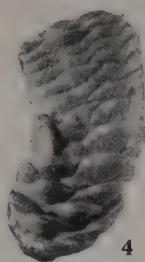
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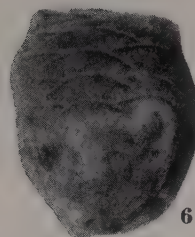
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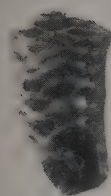
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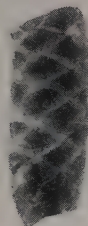
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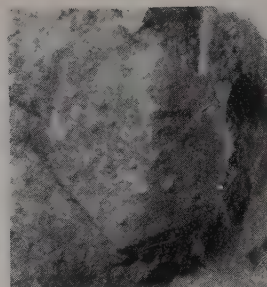
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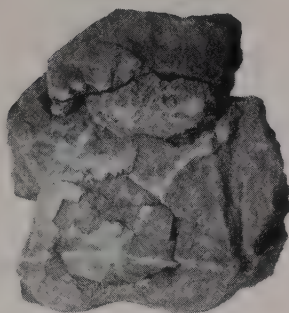
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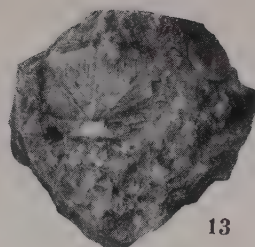
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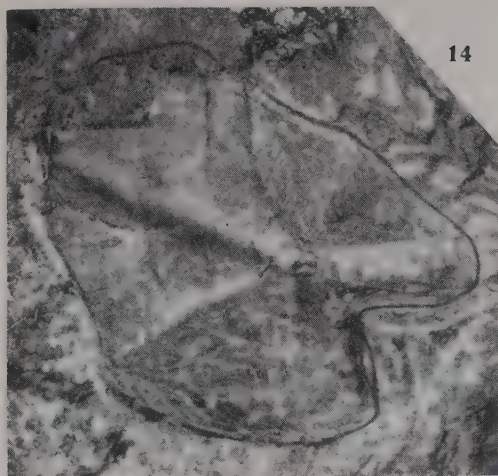
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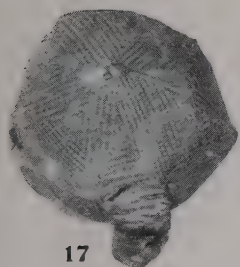
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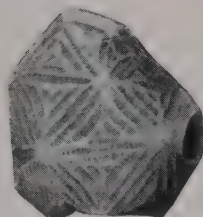
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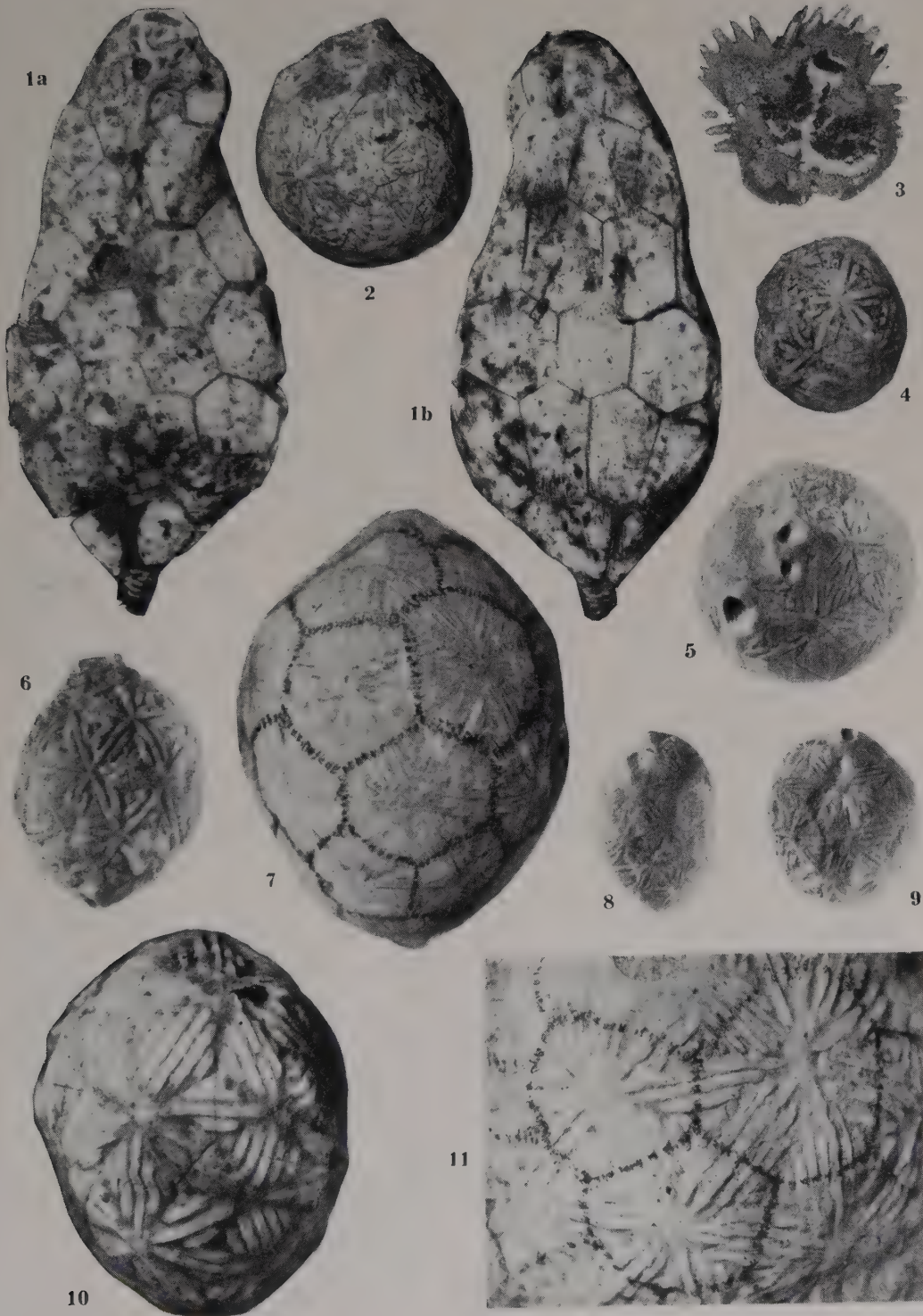
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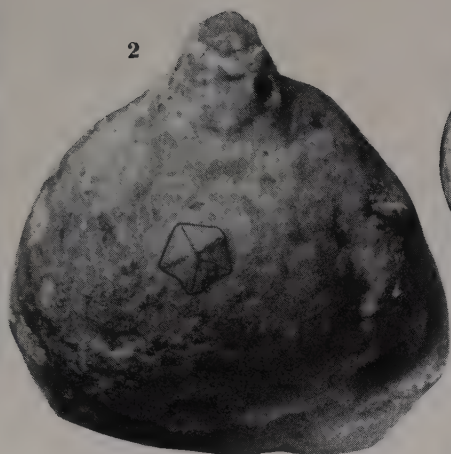








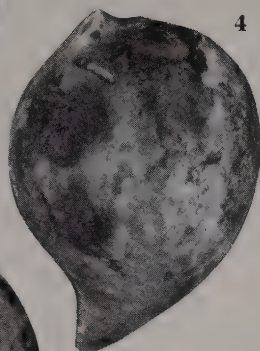
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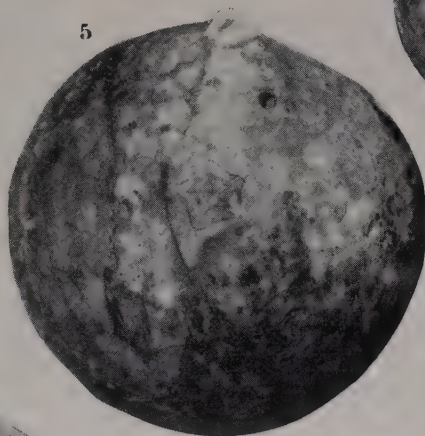
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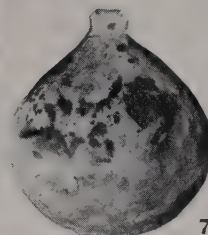
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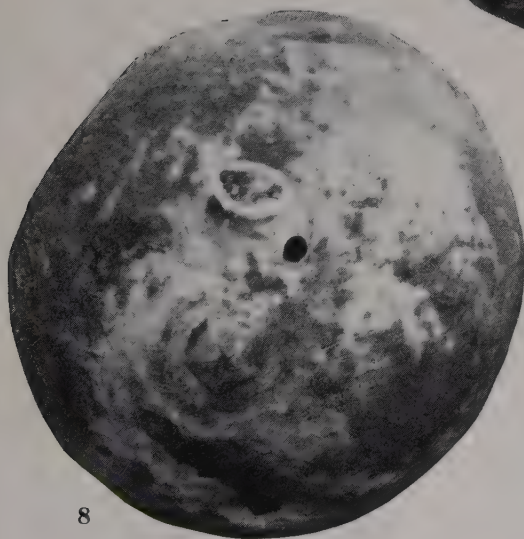
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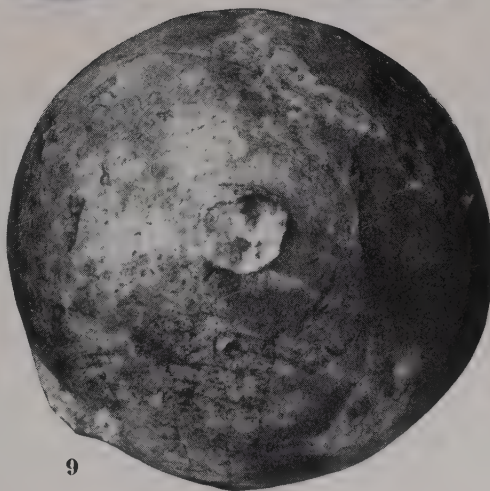
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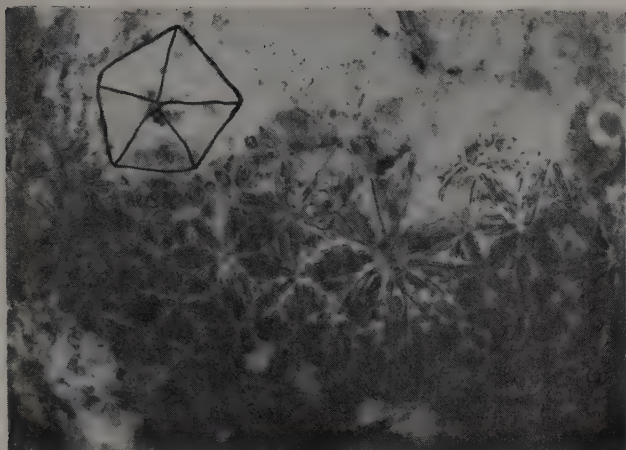
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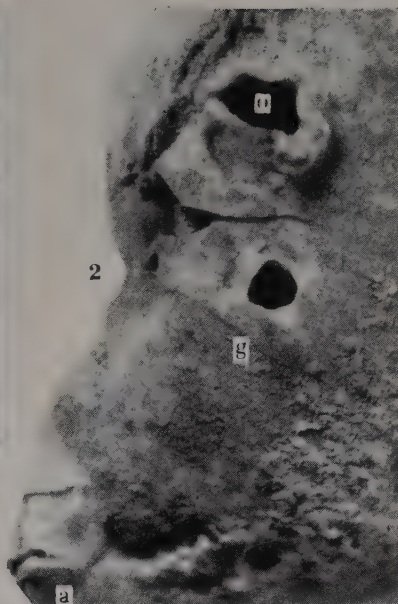
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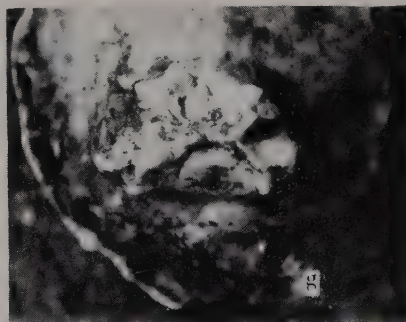
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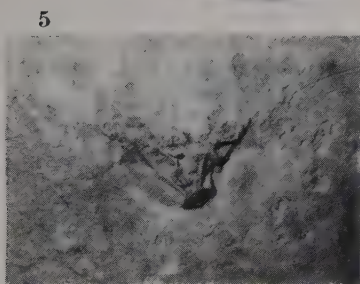
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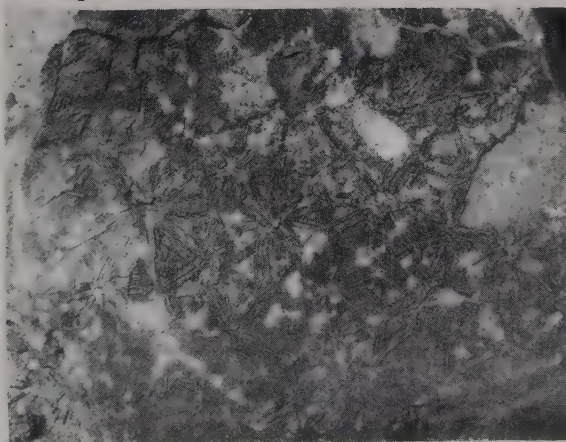
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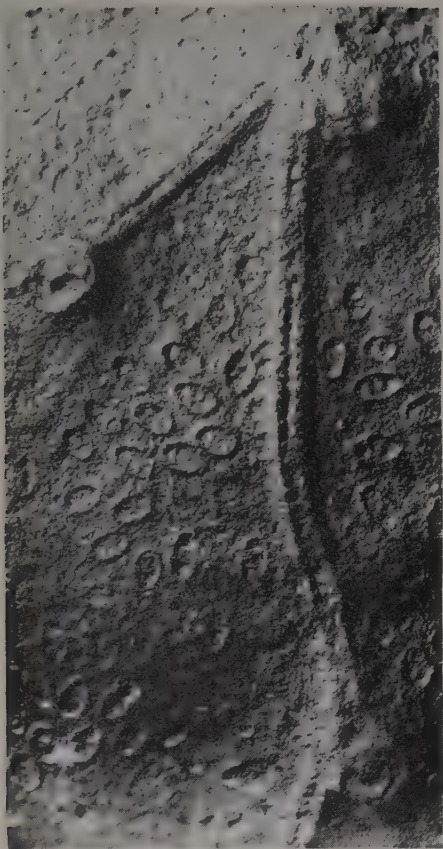
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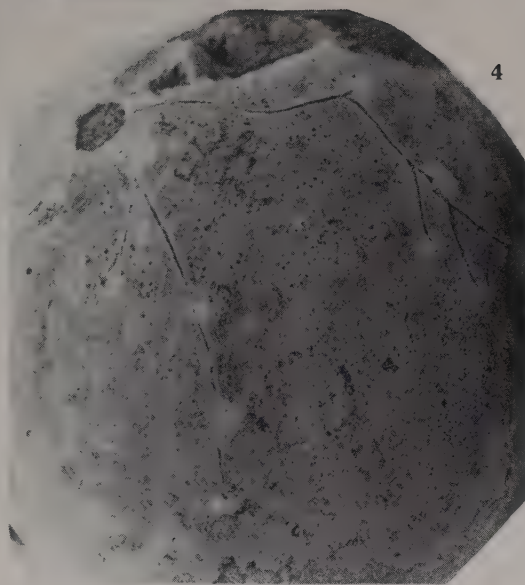
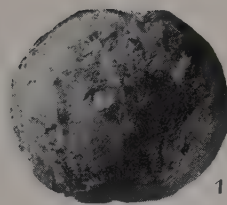
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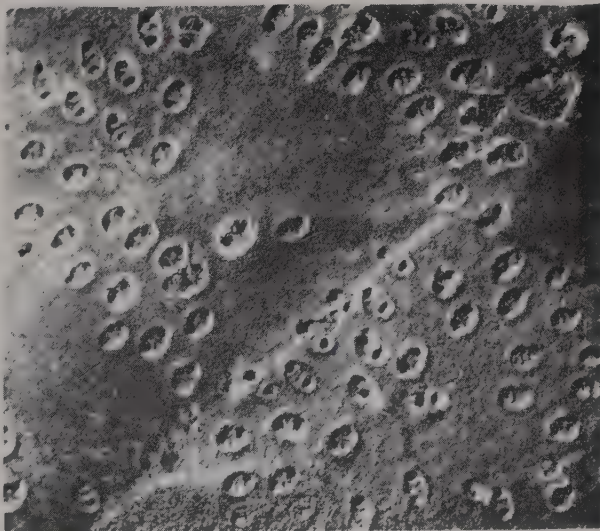




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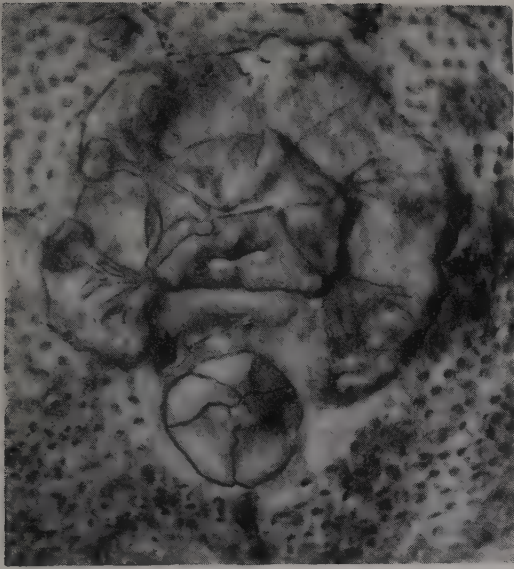
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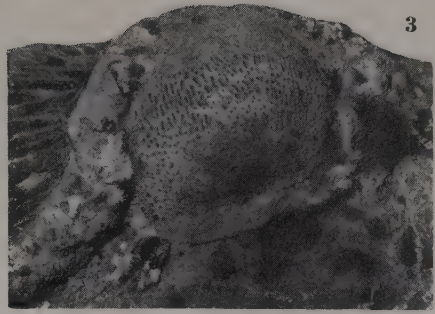




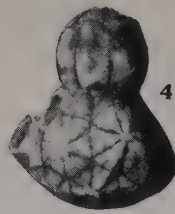




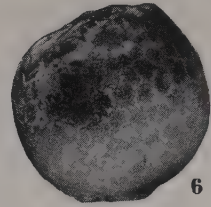
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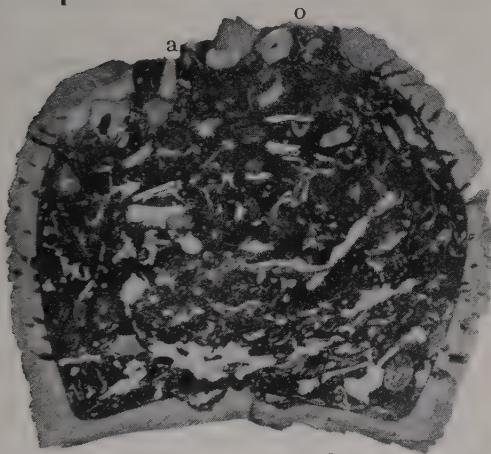
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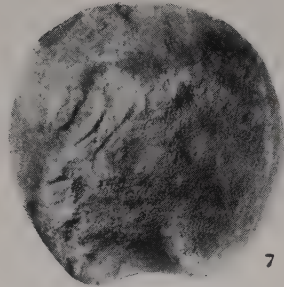
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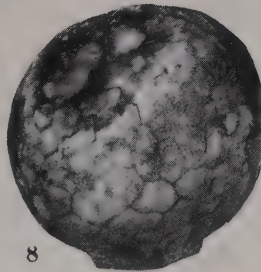
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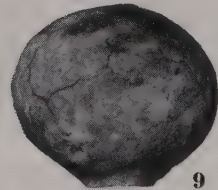
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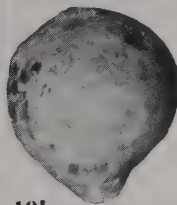
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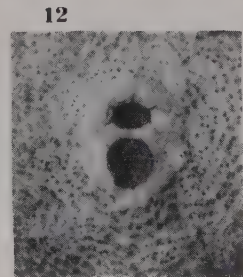
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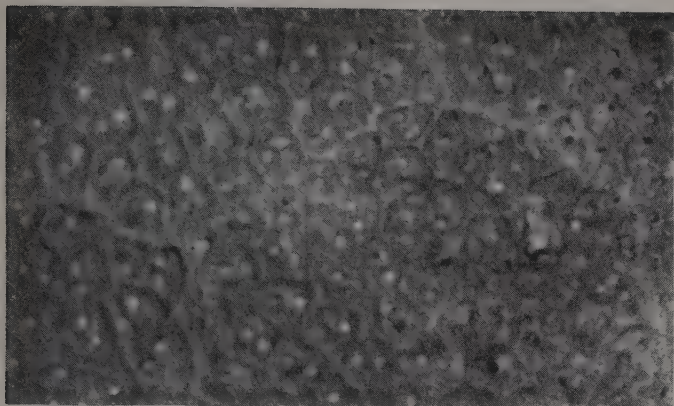
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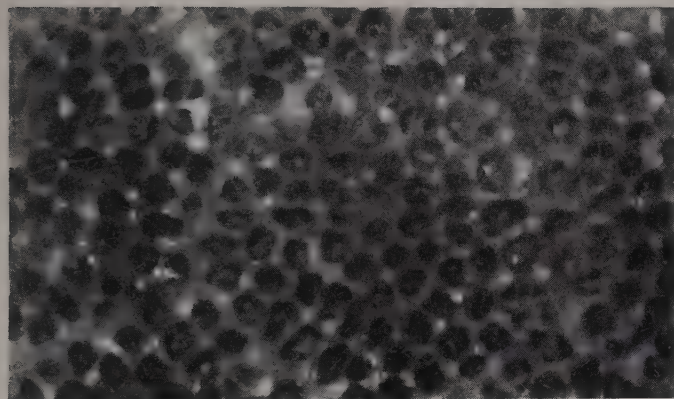
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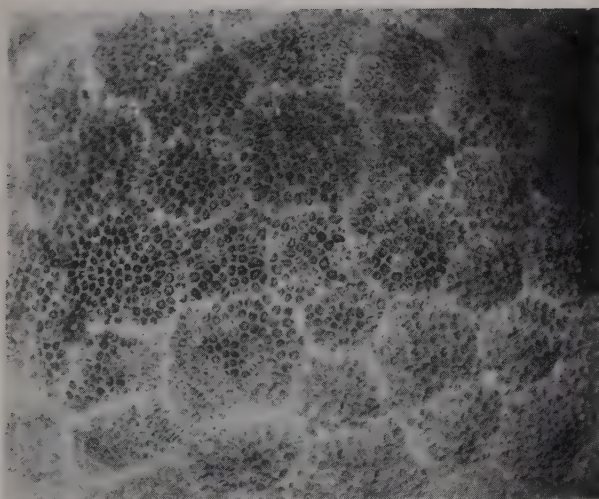




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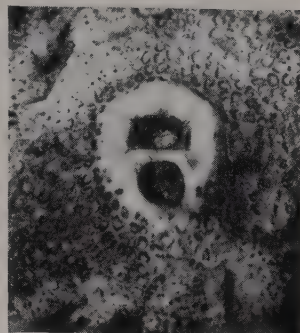
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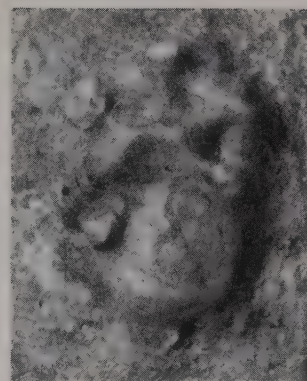
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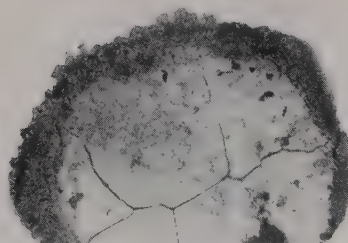
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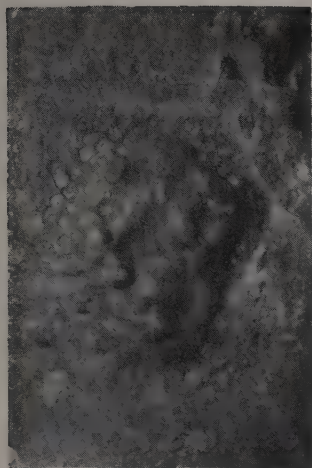
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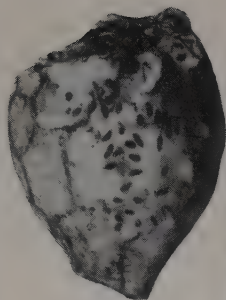
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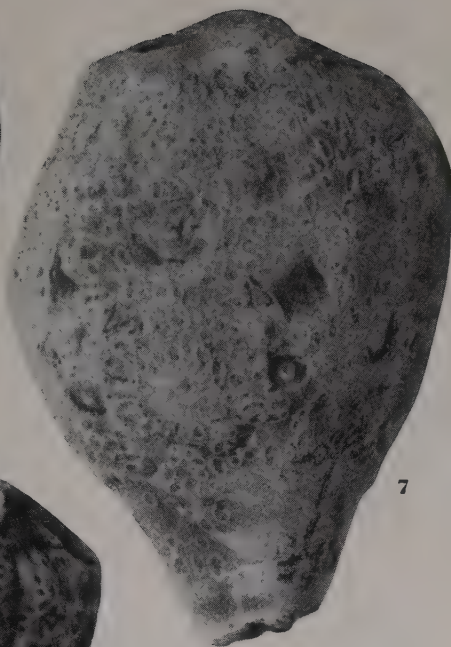




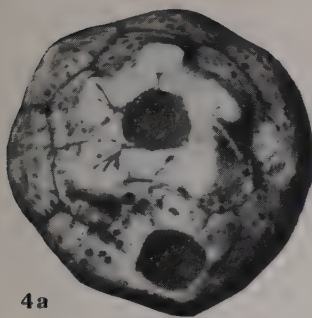
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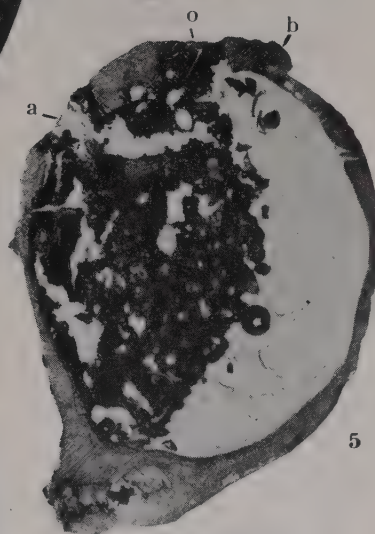
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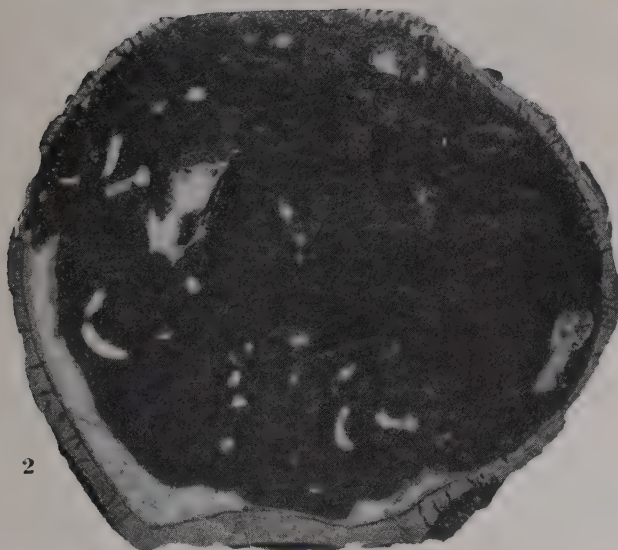
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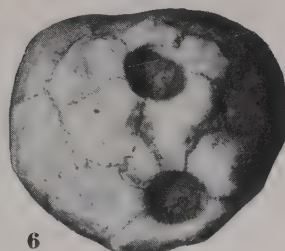
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5



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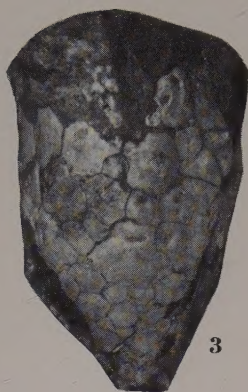
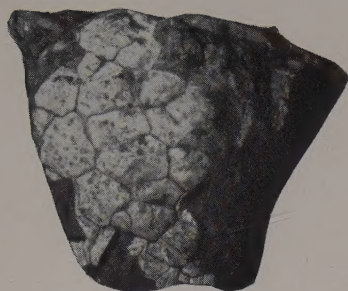
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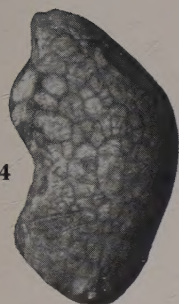




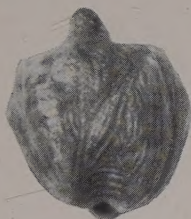


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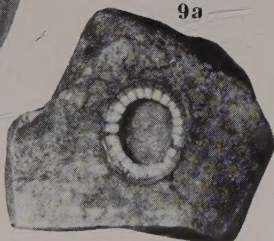
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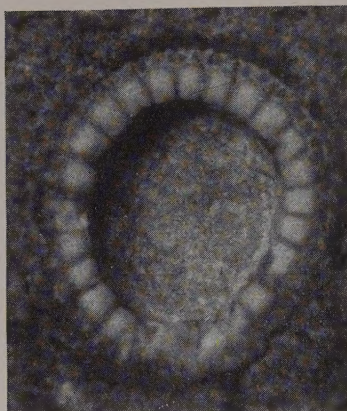
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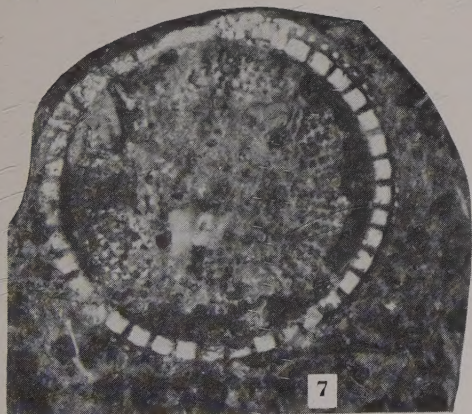
5b



9a



9b



7



8







*Pris kronor 12: —.*